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THE SKELETAL SYSTEM OF NECTURUS MACULATUS Rafinesque.

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9. The Skeletal System of Necturus maculatus Rafinesque.

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Introduction.

In view of Gaupp's recent revision of Die Anatomie des Frosches, Professor von Bardeleben says, "Es wäre im Interesse einer besseren Fundamentirung der vergleichenden Anatomie höchst wünschenswert, wenn bald zu den wenigen ausführlichen Monographien von Wirbeltieren einige neue, z. B., je eines Selachiers, Ganoiden, Teleostiers . . . . eines Urodelen . . . . einiger Reptile und niederen Säuger, besonders Insectivoren, kämen. . . . Wer wagt es?" The following paper is an attempt to carry out the suggestion of the above quotation as far as it concerns a Urodele; and it is hoped that, as occasion allows, papers upon the other systems of Necturus may be added to this and thus gradually complete a monograph upon the anatomy of a typical tailed amphibian.

In the selection of Necturus to serve as a type, I have been guided by several reasons, mostly of a practical nature. *Necturus maculatus* is probably the most abundant and widely distributed Perennibranch in the world, and owing to this fact, as well as to its large size, is employed as universally in American laboratories, as is the *Salamandra maculosa* in Europe. This exploitation of the species as a laboratory animal has led to the development of means for its capture in quantity for such purposes, and it is thus by no means so uncommon an object of study in the laboratories of Europe as it was a few years ago.[1]

Anatomically and structurally considered, the choice of an animal to represent the Urodela should be either that of a highly specialized one, thus emphasizing those characters which are essentially Urodelan; or that of one taken from the most primitive group, which would have the two advantages of showing each organ in its simplest condition, and of suggesting the phylogenetic origin and relationship of the entire order.

Granting that the second of the above alternatives has the most in its favor, the choice would be limited to one of the *Proteidae*, a family represented by three generic

[1] Necturus is supplied at present at most of the American universities at $10.00 per hundred, and although just at present there is an attempt being made by dealers to advance the price, especially of those exported to Europe, such conditions cannot last long.

groups, which are partially or wholly subterranean in their habits and thus modified in various degrees to conform to this environment. Proteus is an inhabitant of certain caves in Austria, and shows, among other troglodytic characters, reduction of eyes, loss of pigment, and a pronounced attenuation of body and limb, the latter combined with a loss of toes. These aberrant characteristics are still more marked in the recently discovered Typhlomolge, which occurs in a subterranean river in the state of Texas. The third and last member of the group, Necturus, occurs in the Great Lakes and other open waters, and, corresponding to its freer life, shows the least modification. It remains by day beneath stones or in subterranean burrows constructed by itself in the mud, and becomes active at night, swimming through the water in search of prey. Its body and legs are robust, and do not show the slender proportions seen in Proteus and Typhlomolge. Its eyes, though small, are functional, and it is well pigmented, especially above. It is thus at the same time a representative of the lowest group of Urodeles, and one not extremely modified.

The genus Necturus is exclusively North American and includes but one common species, *N. maculatus* Raf., although the series of synonyms, as well as some variability of marking, have combined to give the general impression that there is a large number.

Aside from *N. maculatus* Raf., Cope enumerates a second species, *N. punctatus* Gibbes, of rare occurrence and found only in the waters of North and South Carolina.

Necturus maculatus, the subject of this memoir, is a widely distributed form and occurs in abundance in the Great Lakes and their tributaries, and throughout the entire Mississippi valley, as well as in many of the river systems of the Atlantic slope, and those flowing into the Gulf of Mexico. Its abundance and extensive distribution have led the United States government to conduct experiments relative to its introduction as a "food fish," thus far with satisfactory results. In form and appearance it is similar to that of a larval salamandrid, and is subcylindrical, body slightly and head markedly depressed, with three large and bushy external gills upon each side, having two gill slits between them, and with four decidedly robust legs, each with four toes. The tail, which does not exceed half the length of the body, is compressed and surrounded dorsally, caudally, and ventrally by a caudal fin, rounded in outline at the tip. Sexually mature adults seem to be fairly constant in size, varying in total length between about 27 cm. and 34 cm.

The color markings of the integument are due to scattered pigment cells, the variations in the frequency and size of which result in the formation of all possible shades between no color at all and dense black spots. As these cells are very large, and in most places evident to the unaided eye, the principle is seen upon close inspection to be similar to that of a modern half tone illustration, which a careful scrutiny resolves into a series of black dots, although in the latter case the darker shades are due to increased size, and in

the former to an increased number of the elements involved. The ground color of the skin, as may be seen on the ventral side, which is mainly free from pigment, is yellowish or pinkish, but over the sides and back varying degrees of pigmentation produce different shades of slate color, in places with a distinct bluish or purplish tint. The deepest pigmentation is that of the dorsal side where certain densely pigmented areas form irregularly rounded black spots upon a bluish-slate background, thus suggesting the specific name of "*maculatus*."[1]

The skeleton consists of several independently separable portions and, like that of other Urodeles, contains a large amount of unossified hyaline cartilage. By far the largest portion consists of the vertebral column, the skull, to which is attached the hyobranchial complex, and the posterior extremities, which are attached by the ilia to a single sacral vertebra. The two halves of the shoulder girdle are free from one another and from the rest of the skeleton, and they, with their corresponding free limbs, form two distinct skeletal parts. The remaining skeletal elements are the nasal and optic capsules, the two laryngo-tracheal cartilages, and the series of rudimentary sternebra which lie in the mid-ventral thoracic region. All of these latter parts are wholly cartilaginous and entirely disconnected from other parts of the skeleton.

In arranging the descriptive material of this memoir, the above practical division of the skeleton has been taken into consideration as well as the more usual morphological one, and it has seemed best to arrange the subject in the order following. In this the vertebral column will be first treated, together with the ribs and sternum. The visceral arches and the free sense capsules will be treated with the skull, and the limbs and their girdles will appear last. This brings the parts together in their topographical relationships and will be found more practical than a wholly morphological division.

The Vertebral Column.

General Description.

The vertebral column, as is the case with fishes, shows little regional differentiation, since the limbs are too small and weak either to modify the motions of the trunk by the muscles attached to them, or to bring their places of attachment into prominence as points of leverage or support. The only gain in this respect over the condition seen in

[1] Just as this manuscript leaves my hands, I have received from Mr. Alexander Nielsen, of Venice, Erie county, Ohio, an extensive dealer in Necturus, a specimen having a totally different coloring from the usual one, and Mr. Nielsen, who has caught thousands of specimens, writes that it is the first of the kind he has ever seen. The ground color of this specimen is a light reddish buff, with no suggestion of the usual dark slate color. The back is covered with dark brown spots, smaller than in the normal forms. In form and size it closely resembles the common species.

fishes is the direct attachment of the pelvic girdle, which by the medium of a specialized pair of ribs, becomes articulated to a single vertebra, usually the 19th. This vertebra, the sacral, lies naturally in the cloacal region and it seems a matter of doubt whether, as in higher forms, to consider it the boundary between the trunk and the tail, or whether as in fishes, to limit the latter region to those vertebrae which bear closed haemal arches, the first of which is usually the fourth vertebra posterior to the sacral one, *i. e.*, the 23d. The first of these alternatives seems the more natural and open to the fewest objections, for, while it places the first few caudal vertebrae in the same list structurally with those of the trunk, from which, indeed, they are practically indistinguishable, it avoids the equally great embarrassment of leaving the same number as a nameless and anomalous group intervening between the sacral and caudal regions, a relationship unlike anything occurring elsewhere among vertebrates.

The statements given above, that the two vertebrae which have a definite distinction, the sacrum and the "first haemal arch vertebra," are usually the 19th and 23d respectively, suggest variation in this order, a matter which has been made the subject of papers by G. H. Parker ('96) and Bumpus ('97), and has been referred to by Waite ('97).

Regarding the sacral vertebra, according to the first two authors it was the 19th in 65% of 127 specimens examined, the 20th in 27% and in the remaining 8% it was placed "obliquely," that is, with an attachment to the 19th vertebra upon one side and the 20th upon the other. This obliquity is usually sinistro-dextral, *i. e.*, with the left sacral rib in advance of the right (left, 19th; right, 20th). Out of eight such oblique specimens examined by Bumpus, seven were sinistro-dextral, and only one dextro-sinistral. Parker's two specimens were both sinistro-dextral.

Waite describes three oblique specimens, which show for the most part additional abnormalities. In one of these the right sacral rib was on the 19th vertebra and the left on the 20th, thus making the direction dextro-sinistral. In the other two cases the right rib was on the 18th, a case not found by the other authors named, and the left on the 19th, again dextro-sinistral.

Waite also figures a case with two normal sacral ribs on the 19th vertebra, and an additional smaller rib upon the right side of the 20th, also attached to the ilium.

A similar variation occurs in the position of the 1st haemal arch, although a careful comparison by Bumpus has shown that variation here is entirely independent of that of the sacral vertebra. Out of 98 specimens examined with reference to this, the 1st haemal arch was borne on the 22d vertebra in 11 specimens, on the 23d in 82, and on the 24th in 5.

The variation in the total number of vertebrae, which is considerable, is seen to be mainly that of the caudal region, as it has been shown that there is a variation of but two

vertebrae at the sacrum, and but three at the first haemal arch. The results of counting the vertebrae in 100 specimens are expressed by Bumpus in the following table:—

No. of vertebrae.	No. of specimens.
43	2
44	9
45	21
46	18
47	14
48	16
49	11
50	5
51	4
	100

By this it will be seen that the average total number is 45 or 46.

A Typical Vertebra.

In order to understand the structure of the separate vertebrae, any trunk vertebra except one of the first two or three may be selected as a type and its parts studied in detail, after which the differences seen in other regions may be noted, and a few special vertebrae selected as worthy of individual study. The 16th vertebra has been selected for this purpose, and four views are given of it in text figures 1–4. These figures were drawn from a dried vertebra prepared by maceration in caustic potash and hence lack the cartilaginous portions and other related soft parts referred to in the text.

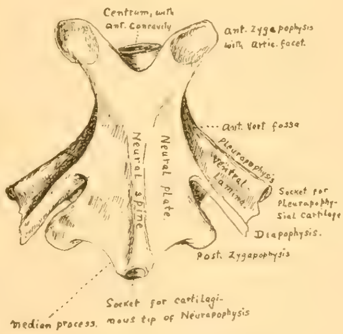

Fig. 1. 16th vertebra; dorsal aspect. × 3.

This vertebra consists primarily of a ventrally situated centrum or body; a neural arch, the dorsal aspect of which is broadened out into a broad, flat plate; and upon each side a complicated transverse process directed backwards and bearing a short rib which articulates with it in two places.

The centrum is in the form of a slender hour glass, its ends marked by very deep cup-shaped depressions, thus making the entire vertebra con-

spicuously amphicoelous. In the recent state these depressions are filled in with portions of the original notochord which become restricted to these intervertebral segments by the development of the osseous vertebrae. Corresponding to the shape of the space included by two approximated ends of vertebrae, these notochordal segments are in the shape of two cones placed base to base, the place where the two bases meet being the line of separation between the two vertebrae involved.

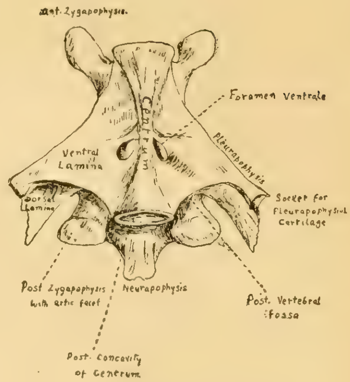

Fig. 2. 16th vertebra; ventral aspect. × 3.

The neural arch is much flattened dorsally, and its sides, the neural laminae, become so much obscured by fusions with the elements of the transverse process that they are seen distinctly only when the vertebra is viewed from one end. The main bulk of the arch consists of a flat neural plate, which in a dorsal view of the vertebra nearly conceals the rest. This plate is approximately a rectangle with sides a little incurved. Anteriorly its corners become prolonged into a pair of rounded anterior zygapophyses, and posteriorly it develops a pair of somewhat similarly shaped posterior zygapophyses, between which extends a short, median process. As the posterior zygapophyses of each vertebra overlap the anterior ones of the next succeeding, the articular surfaces of the former lie upon the ventral, and those of the latter upon the dorsal aspect. At the blunt posterior point of the posteriorly directed median process, there is a small cup-shaped depression filled, in the recent state, with a nodule of cartilage which forms the tip of the neural spine, the osseous continuation of which extends along the median line of the neural plate, becoming obsolete anteriorly.

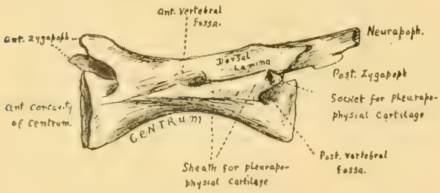

Fig. 3. 16th vertebra; left lateral aspect. × 4.

The term "transverse process" is a convenient name by which to distinguish certain composite and irregular masses placed upon either side of the centrum and bearing the proximally forked ribs. Each transverse process consists essentially of two cartilaginous rods, dorsal and ventral, encased in an irregular bony mass. Of these two rods, the dorsal one, the diapophysis, proceeds from the side of the neural arch, while the ventral

one, the pleurapophysis, is associated with the centrum. The investing bony mass is formed secondarily about these rods by periostosis and consists essentially of two simple investing sheaths and two flattened laminae, of which one is vertical and dorsal, connecting the two sheaths, and the other horizontal and ventral, applied to the ventral side of the pleurapophysial sheath and spreading out proximally over nearly the entire length of the centrum, with which it becomes fused. This latter lamina is perforated by the ventral foramen, situated immediately posterior to the pleurapophysis and transmitting the collateral vertebral vessels. As the dorsal lamina meets the ventral one nearly at right angles, they form with the side of the centrum, two fossae, the anterior and the posterior vertebral fossae. The posterior fossa is much the deeper and communicates with the region ventral to the vertebral column by means of the ventral foramen just mentioned.

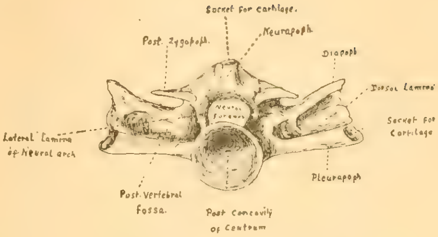

Fig. 4. 16th vertebra; posterior end view. ×3.

In the larva the cartilaginous diapophysis and pleurapophysis are directly continuous proximally with a lateral mass, the "rib bearer" (Rippenträger) of Göppert, while distally they unite to form the cartilaginous rib, the whole mass being at this time a continuous piece. The process of ossification within and around the rib bearer and the sides of the vertebrae, and especially the growth of the osseous sheaths about these rods, gradually cut them off from one another and restrict them proximally into tapering points, so that in a macerated adult vertebra, from which all the cartilage has been removed, the moulds of the parts in question are seen as very deep and conical pockets.

Later ossification separates the free rib from the encasing sheaths of the transverse process, and joints are thus formed between the two bodies. The part of the rib thus segmented from the diapo hysis forms the tubercular process and the part once in connection with the pleurapophysis becomes the capitular process, both processes retaining throughout life an articular connection with the rods from which they originally separated.

Embryological investigation has rendered it probable that the pleurapophysis and its associated capitular head represent the primary condition, and that the cartilage of the rib bearer becomes dorsally extended for increase of support, developing later the secondary or tubercular attachment. Göppert has shown this secondary growth of the tubercular connection in the case of Triton and some other Urodeles, a growth which proceeds from the ribs and follows along a line of connective tissue until it reaches the rib bearer

at its dorsal prolongation, applied to the side of the neural arch. As he expresses it in his summary, "Die dorsale Spange ist ein verlängertes Tuberculum, das im Dienst einer ausgiebigeren Befestigung der Rippe steht." Unfortunately he fails to find this dorsal connection in Necturus, and states that "der dorsale Theil des Querfortsatzes tritt nicht so deutlich als ein Balken hervor wie bei Salamandra und entbehrt auch hier der distalen Höhlung, da die dorsale Rippenspange den direkten Anschluss an den Querfortsatz nicht erreicht."

As shown below, and in several of my figures, this "distale Höhlung" at the tubercular articulation of the transverse process is often very evident, and through the medium of the enclosed cartilaginous rod, articulates with the tubercular process of the free rib. Göppert's description ('96, p. 398) of the condition in Salamandra corresponds so completely with that of the adult Necturus that it could well be substituted for the description given in this work. The "Abweichungen" which he finds in Necturus do not exist.

A summary of the main features of a typical vertebra and its relations to other parts of the skeleton may be given as follows: —

1. Osseous elements. Centrum; neural arch, including dorsal plate and lateral laminae; transverse process, including sheaths of rib bearers, and the associated dorsal and ventral laminae.

2. Cartilages and other soft parts. Two pairs of lateral rods or rib bearers; a neural spine; intervertebral notochordal cones.

3. Articular surfaces. Two for the centrum; two anterior and two posterior zygapophyses; two tubercular and two capitular articulations for the corresponding heads of the ribs.

Comparison with Other Vertebrae.

A study of the separate features brought out in the above description, as they occur in the rest of the vertebral column, yields the following results. These, for the sake of brevity, are expressed somewhat in the form of a table in which a few obvious abbreviations are employed. Thus the vertebrae are expressed by consecutive numbers, beginning the enumeration with the atlas, which is 1; S is the sacral vertebra (19 or 20), and H is the first one bearing a haemal arch (22 to 24).

Neural and haemal spines. — The neural spine forms a prominent ridge in 1; somewhat depressed and rounded at the end in 2. The neural spine of 3 shows the maximum of size in the trunk vertebrae and is here the most erect, *i. e.*, makes the greatest angle

with the longitudinal axis of the vertebra. From there as far as S, it is gradually smaller and more depressed. After S it becomes again larger and more erect, so that the spine of 21 is about equal to that of 3, and that of 22 surpasses it. It rapidly lengthens as far as 26 to 27, where it reaches its maximum of length and is about equal to the haemal spine; from then on, both neural and haemal spines become gradually reduced as the vertebrae diminish in size.

A haemal spine appears suddenly on the 22d to 24th vertebra, usually the 23d, an indication of it sometimes being found upon the previous vertebra in the form of a thin bony bridge which stretches across the ventral face of the vertebra from the outer angle of the transverse process to the centrum, thus covering the posterior portion of the ventral lamina. In one case noted, the vertebra just anterior to H bore upon one side a slender process, 4 to 5 mm. long, evidently representing an incomplete haemal arch. The first haemal spine is of about the maximum size, and, after three or four vertebrae in which this size is maintained, the haemal spines begin to diminish with the gradual reduction of the vertebrae, as in the case of the neural spines. The neural and haemal spines of the same vertebrae closely resemble one another, but, in the first few vertebrae that possess both, the former take a slightly more erect position while the latter lie more nearly parallel to the axis of the vertebrae. Towards the end of the tail both neural and haemal spines sometimes appear bifurcated at the tip, or even double as far as their base. In a given vertebra this may affect either spine alone or both spines.

Zygapophyses.— In 1, the anterior zygapophyses are wanting and the posterior are near together. From 2 to S both sets are divergent and almost identical, save that the entire vertebrae at about 15 to 17 are a little wider than elsewhere and hence the zygapophyses are here farther apart. After S the vertebrae rapidly become narrow, and, beginning with H, both sets approach very near together and are reduced in size. They become obsolete at about 26, beyond which the vertebrae articulate solely by means of the vertebral centra.

Ventral foramina.— These do not appear in the three anterior vertebrae and are usually of small size in 4. From then on, as far as H, there is usually a pair in each vertebra, although occasionally the foramen of one side may be converted into a notch by a deficiency in the ventral lamina. In H, where the roots of the haemal spine form thin laminae lying over the region of these foramina, openings occur not only in the ventral laminae as usual, but also in the laminae connected with the haemal spine, and the two sets of foramina are accurately superimposed. Beyond H the reduction of the entire transverse process renders the ventral foramina unnecessary, but in the two or three vertebrae succeeding H the new foramina through the base of the haemal spine may be present, although usually appearing upon but one side.

Transverse processes. — These processes, quite rudimentary in 1, are represented in 2 by the dorsal lamina alone, while the ventral lamina appears but slightly indicated by a curving in of the ventral margin of the former. A continuation of this method produces in 3 a fair indication of a ventral lamina, which in 4 has become of normal size and appearance. In vertebra 2 to 7, approximately, the dorsal laminae are set perpendicularly, beyond which they grow more and more oblique. In the sacral vertebra they become again nearly perpendicular, beyond which they rapidly become obsolete but remain more nearly perpendicular. As they degenerate they separate into two portions, a dorsal and a ventral, corresponding to the diapophysis and pleurapophysis (Göppert's "Balken"). This division occurs at approximately the 25th vertebra, after which the dorsal or tubercular portion disappears in 2 to 3 more vertebrae, while the ventral or capitular portion persists for a few vertebrae farther.

Attachment of ribs. — As shown above, the ribs are bifurcated at their proximal ends, the two being known as the dorsal or tubercular and the ventral or capitular attachments. These relations of the soft parts are plainly indicated in dried specimens by the presence and relative development of the sheaths, the laminae of which furnish a set of moulds giving the exact condition of the cartilages, and thus the following items, although obtained for the most part from dried specimens, will doubtless be found to be wholly reliable. Vertebra 1 is entirely without ribs. In 2, 3, and 4, both tubercular and capitular ends of the ribs are of large caliber and both are attached to cartilaginous rods. In 2 the capitular sheath is exceedingly small and the tubercular one a little larger. In 3 the tubercular sheath is quite large and the capitular one a little smaller, and in 4 both are large, the capitular sheath being slightly in excess of the other. From 5 to 8 the capitular sheath is always present but there is no distinct tubercular one, this attachment being one of simple osseous contact. In the sacral vertebra there are two sheaths, one for each attachment. They are of about equal size and are larger than in any other vertebra. These two attachments of the sacral rib are figured and described by Göppert ('**96**, p. 402), but, since he has failed to find them in the other vertebrae and has even stated that a tubercular attachment does not exist, he is under the necessity of accounting for them in some other way. This he does by describing a process (Höcker) which grows out of the side of the rib bearer, and "dient der Befestigung der kurzen oberen Spange der Sakralrippe." Although these words are noncommittal, the implication is, that this "Höcker" and the connection thus formed are a new formation and not homologous with the dorsal or tubercular connection. This leads to the inevitable conclusion that the dorsal or tubercular connections of the sacral ribs are not homologous with those of the others, a conclusion which a moment's consideration of an entire adult skeleton would render invalid. The vertebrae which intervene between the true sacral vertebra and the

one bearing the first haemal arch, vary considerably in their relation to costal elements. The first of these vertebrae in many cases bears a small pointed rib with a capitular attachment alone, but this seems to be more usual in cases in which the sacral vertebra is the 19th. In one such case with the first haemal arch upon the 22d vertebra, the 20th bore small ribs and upon the 21st appeared very minute capitular sockets, which, as this was a macerated specimen, might have originally borne rib rudiments. There seems to be much variation in these as well as in other particulars in this very variable region, but the specimens examined have been too few in number to give any general conclusions.

Study of Special Vertebrae.

Atlas.—The main characteristics are the reduction in total length to about one half that of a normal trunk vertebra, the peculiar shape of the centrum, the rudimentary condition of the transverse process, and the conspicuous and projecting neural arch. The posterior end of the centrum is normal but anteriorly it broadens rapidly to form a wide wedge, the base of which is directed forwards and bears the two condyles. These are slightly concave, elliptical surfaces, inclined a little outward, and meeting in the median line where a small but conspicuous tubercle is formed that fits into a space upon the ventral side of the skull between the two exoccipitals. The ventral aspect of the centrum is somewhat hollowed and a little roughened for muscular attachment, a peculiarity shared by the 2d vertebra. The neural arch is large and conspicuous. Its sides are flattened and obliquely set, and it ends in the mid-dorsal line in a rounded edge or keel, the posterior end of which bears a small socket for the cartilaginous tip of the neural spine, as in other vertebrae. The two posterior zygapophyses are large and heavy. The transverse processes are rudimentary and very variable, even upon the two sides of the same vertebra. Their most constant parts are a usually bifurcated piece projecting obliquely backwards in the same position as, and probably homologous with, the dorsal lamina of the succeeding vertebrae; and a much shorter spine, placed ventral to this and also projecting backwards. The larger process is pierced by an obliquely directed foramen which communicates with the neural canal and transmits the internal carotid artery and the first pair of spinal nerves.[1] Between this process and the short ventral spine there is a narrow but very deep fossa. By the bifurcation of the original transverse process and the addition of the spine ventral to it, there are formed three backwardly directed processes which

[1] Hoffmann suggests that the phenomenon of a pair of spinal nerves boring through the substance of a vertebra in an animal in which the nerve exits are normally intervertebral, is an indication that the "atlas" really represents two fused vertebrae, the line of separation being marked by the nerve and its foramen.

are very variable in their mutual relations. Occasionally all three will be distinct and of about the same size, but usually the ventral spine is much smaller than the other two. There may also be varying degrees of bifurcation of the genuine transverse process, or it may present one or more small processes in addition to the usual three.

Vertebra bearing the first haemal arch. — This is normally the 23d in the series, but it may be the 22d or even frequently the 24th. After the sacrum, the neural plates rapidly narrow, and, by the time the vertebra in question is reached, this part has become about as narrow as the base of the neural spine, so that the latter appears in direct continuation with it, the posterior zygapophyses appearing as lateral processes borne upon the sides of the spine. This increase of the apparent length of the neural spine renders it strikingly similar to the haemal spine, and thus is seen the first suggestion of that dorso-ventral bilaterality which becomes so marked in the more posterior caudal vertebrae. The transverse process is thin and poorly developed, and the occasional bifurcation of its free end gives an indication of its division into tubercular and capitular portions as seen in the vertebrae immediately posterior to this. The haemal arch, which is a new element and thus gives distinction to this and the following vertebrae, begins as a pair of low, thin ridges springing from the ventral side of the centrum and uniting across the mid-ventral line near the posterior limit of the vertebra in such a way as to frame in a haemal foramen just ventral to the centrum, which, with the foramina of the succeeding vertebrae, forms the haemal canal. The ventral laminae are perforated as usual by the two ventral foramina, and, as they are nearly covered by the two ridges that form the roots of the haemal arch, a pair of foramina occurs also in these latter opposite the usual ones. In most instances the first haemal arch appears, as it were, suddenly and perfectly developed, and the vertebra immediately preceding the one that bears it usually shows no suggestion of such a structure. Occasionally, however, a rudiment of the foot or root of the arch appears upon one or both sides of the previous vertebra in the form of a thin plate lying parallel to the ventral lamina, and extended across from centrum to outer end of the transverse process, and, in one instance observed, a slender haemal process appeared upon the left side, which projected back over the following vertebra and plainly represented one side of a rudimentary haemal arch. There was no trace of this upon the other side.

The caudal vertebrae posterior to the above, with especial reference to the terminal ones. — The most conspicuous characteristic of the caudal vertebrae posterior to the above is the presence of nearly equal neural and haemal arches running out into long spines with their free ends pointed obliquely backwards. The reduction of the transverse process, which begins just posterior to the sacrum, progresses rapidly after passing the first haemal arch. The process first becomes divided into its two portions, the dorsal one

of which survives but two or three vertebrae, while the ventral one continues for two or three more. *Pari passu* with the loss of the transverse processes, the zygapophyses become reduced and finally disappear. With the loss of these lateral elements the vertebrae become narrowed from side to side, and, as this appearance is further increased by the great extension of neural and haemal arches and spines, the entire column becomes strongly compressed laterally, thus corresponding to the change in external form which is so apparent in the living animal. In this more characteristically caudal region (*circa* between 28 to 40) the hour glass shape of the centra becomes more apparent and in the reduction which follows towards the tip, this element becomes more and more conspicuous as the main portion of the vertebrae. Thus, after about the 40th vertebra, rapid reductions take place in the arches, both neural and haemal, and the terminal one or two vertebrae consist of centra alone, the posterior end of the final one being rounded and without the characteristic cup. In this loss of arches it seems that the neural arch disappears first, as in all the cases examined several of the last vertebrae consisted of body and haemal arch alone, but the specimens examined were too few in number to establish this as a law. From about the point at which the vertebrae first become laterally compressed, or more exactly, after the loss of the zygapophyses, there is shown an almost complete dorso-ventral bilateral symmetry, so that in an isolated vertebra it becomes extremely hard to distinguish between the neural and haemal arches. There is, however, a slight difference which, though difficult of formulation, may be perceived after a little study and seems to consist mainly in a some-

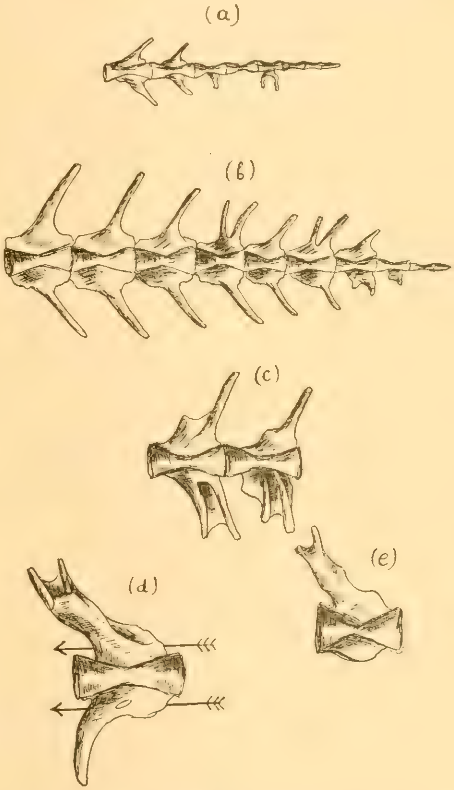

Fig. 5. Caudal vertebrae; (a) and (b) two examples of terminal vertebrae; (c) instances of double haemal spines; (d) and (e) two successive vertebrae in the same series showing doubling of neural spines. The arrows in (d) pass through the neural and haemal canals.

what greater size of the neural canal in comparison with the haemal, and a consequent greater height of the anterior portion of the neural arch, which in this region becomes prolonged and tubular.

A common phenomenon in these last caudal vertebrae, beyond about the 38th, is an antero-posterior bifurcation or doubling of either the neural or the haemal spines or both. Frequent examples of this are noticed in the accompanying figure (fig. 5), in which appear several grades of this malformation, from a bifurcation of the free end to what seems to be a complete doubling of the spine. This phenomenon is referred to by Bumpus ('97) and figured in some of his radiograph illustrations.

Sternum.

The several cartilaginous rudiments which represent this part in Necturus are somewhat difficult of detection and thus entirely escaped the attention of the earlier investigators. They consist of a number of thin cartilages found in several successive myocommata of the pectoral region and confined mainly to the area covered by the overlapping

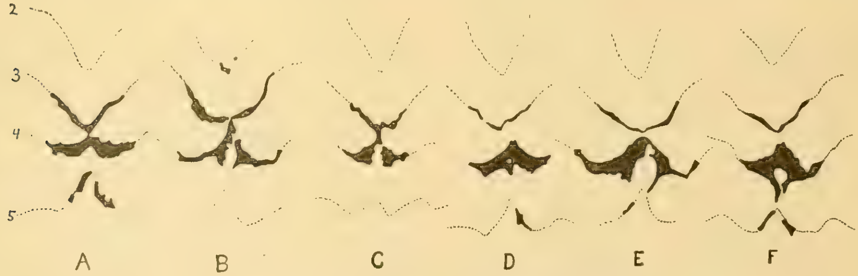

Fig. 6. Sternal pieces of six different individuals, showing variation.

epicoracoids. As will be seen by text figure 6, which represents the sternal elements of six normal individuals, the cartilaginous pieces show great individual difference in shape and size, and are capable of some variation in the myocommata involved. The largest segmental portion or sternebrum is that of the 4th myocomma which is in general an irregularly triangular or often bat-shaped piece. It lies just posterior to the epicoracoids, in the angle formed by their overlapping edges, and is sufficiently large and superficial to give rise to a part of the fibers of the pectoralis muscle. This muscular attachment as well as its position relative to the shoulder girdle fixes its identity as the homologue of

the rhomboidal sternal plate of the higher Urodela, and it would seem probable that this latter has resulted from the development of this piece alone. The sternebrum associated with the 3d myocomma forms a long and slender open V, which may or may not be continuous with the sternebrum of the 4th. Sternal elements are often found both in the 2d and in the 5th myocomma, usually as a pair of cartilages, or as a unilateral piece. Of these, the one associated with the 5th myocomma is much the more frequent, being found in rather more than half of the specimens thus far examined, either upon one side or both. Sternal elements in the 2d myocomma are rarely seen.

Ribs.

These have already been partly described with the transverse processes of the vertebrae. In the larva they are cartilaginous and are directly continuous with the two cartilaginous rods enclosed in the osseous transverse process, and are thus bifurcated at their proximal end. During the later process of ossification the ribs become ossified as separate pieces and the cartilage remaining between the proximal ends of the ribs and the sheaths of the vertebral rods becomes divided across, thus furnishing two sets of articular cartilages. By the shape of the first two ribs in the adult, it would seem that both of the rods are equally involved and simply fuse to form the ribs, but farther down the ventral or capitular attachment retains its full size and importance, while the dorsal one, although more in the same line with the free end, becomes much reduced, and in many vertebrae its attachment is merely ligamentous. Thus, described anatomically, the ribs of the 2d and the 3d vertebrae possess almost equal capitular and tubercular heads, and show a tendency to become bifurcated at their tips. In the ribs of vertebra 4 to 6 the two heads are still almost equal but the distal part of the rib is a simple rod; and farther down, from about the 8th vertebra on, the capitular head forms the main attachment, and meets at a decided angle the straight piece formed by the free end and the tubercular head. The sacral rib possesses two very large and equal heads, but is not bifurcated distally, and beyond the sacrum the rib element is a variable quantity (*v. sup.*). It would thus seem, judging from purely anatomical evidence, that the condition described by Göppert as characteristic of Necturus is not a universal one applicable to

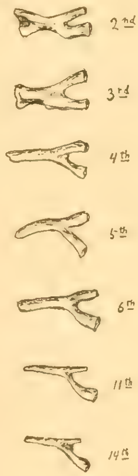

Fig. 7. Ribs taken from the right side of the body and placed so as to show the anterior aspect. The tubercular head is above and the capitular below. The numbers refer to the vertebra to which each rib belongs. × 2.

all of the vertebrae, but is restricted to a certain region, approximately that of vertebra 8 to 18.

It would seem important to investigate the development of transverse process and rib in certain of the other vertebrae, for example the 2d and the 4th. Regarding the sacral vertebra and its rib, as stated previously, Göppert's conclusion, which does not allow a complete homology with the rest of the vertebral column, seems anatomically improbable.

The Skull and Visceral Skeleton.

Anatomically, the bones of the head consist of (1) the skull in the restricted sense, which includes the cranium, the ear capsules, and the upper jaw pieces, (2) the nasal and optic capsules, and (3) the visceral skeleton, represented by the mandible, the hyobranchial apparatus, and the laryngeal cartilages. In point of origin the elements are three in number: (1) the primitive cartilage, still seen in the sense capsules, the primordial cranium, and the most of the visceral skeleton; (2) cartilage bones, or ossifications of localized portions of the primary cartilage; and (3) dermal bones of integmental origin, investing the surface of the cartilage in skull and mandible.

Although there are osseous elements from two sources, the proportion of unossified cartilage left in the adult head is very great and compares in this respect with the condition seen in the Chondrostei rather than with that of other fishes or of most amphibians. This large amount of cartilage is very suggestive of an embryonic or immature form, and suggests either the possibility which has already been frequently expressed, that Necturus is in a sense a permanent larva, as is the case with the Axolotl, or that it is an exceedingly primitive form, perhaps nearer the fishes than any other amphibian.

An orderly treatment of this complex bit of anatomy is extremely difficult and may perhaps be facilitated by the presentation of a classification of the subject, which will be adhered to in the later description.

General Description.
The Chondrocranium.
The Osseous Elements.
- (a.) Otic and occipital regions.
  1. Pro-otic.
  2. Opisthotic.
  3. Exoccipital.
  4. Quadratum.
  5 and 6. Paraquadratum and operculum.

(b.) Brain case.
1. Frontal.
2. Parietal.
3. Parabasal.
(c.) Upper jaw.
1. Maxillary arch.
a. Premaxillary.
2. Palatopterygoid arch.
a. Vomer.
b. Palatopterygoid.
The Visceral Skeleton.
(a.) General morphology of the arches.
(b.) Mandible.
1. Dentale.
2. Angulare.
3. Spleniale.
(c.) Hyobranchial apparatus.
(d.) Suspensorial relations of the hyoid.
The Free Sense Capsules.
(a.) Nasal capsule.
(b.) Optic capsule.
The Teeth.
Comparison of Nomenclature.

General Description of the Skull and its Parts.

The term "skull" is used here in its most restricted sense and does not include either the mandible, the hyobranchial apparatus or the nasal and optic capsules. These elements are for the most part easily detachable from the firmly consolidated skull, and are thus, in the anatomical sense, not to be included with it. A single exception may be made in the case of the nasal capsule with regard to which the usage of authors differs, since, although anatomically distinct in Necturus, it belongs genetically to the primordial skull. Wiedersheim, for example, who is correct from the morphological standpoint, figures it in his drawing of the skull, while both W. K. Parker (in Proteus) and Huxley fail even to find it. In this paper it will be omitted from consideration at present to receive special treatment later on.

The skull, then, denuded of all its extraneous elements, will present an appearance much as is given in figures 2 and 3 (plate 63). The general outline suggested a pentagon to Huxley, but in order to see it as such, one should imagine the ligaments restored that

stretch from the outer end of the premaxillaries to the quadrates. The five angles of the pentagon may be named from the bones that compose them, (1) premaxillary, (2 and 3) two quadrate, and (4 and 5) two opisthotic ; and the five sides in a similar way may be termed (1) occipital, (2 and 3) the paraquadrate, and (4 and 5) the palato-pterygoid. When dissected or macerated sufficiently to show its parts, it gives the distinct and correct impression of a cartilaginous structure overlaid by flat dermal bones laid on and overlapping "like shingles," to borrow Parker's apt comparison, and showing in places certain intervals through which the primordial skull and its ossifications are distinctly seen. When viewed dorsally (pl. 63, fig. 2) the most conspicuous dermal elements are the frontals and the parietals, which form almost the entire roof, and at the anterior end of the former appear the little premaxillaries. Of the maxillary arch, which normally extends from the outer end of the premaxillary to the quadrate, there is no trace, other than a firm ligament when in the recent state, but the inner arch, parallel to this, is well represented by the vomer and the palato-pterygoid, the outer edges of which are seen in the figure. The only other dermal bones visible from above are the paraquadrates which are seen extending along the postero-lateral sides of the pentagon. The dorsal aspect displays also parts of four cartilage bones : the quadrates forming the antero-lateral angles, the pro-otics and opisthotics in the interval between the parietals and paraquadrates, and the exoccipitals which border the foramen magnum and form the condyles. Upon the ventral side (pl. 63, fig. 3) the most conspicuous bone is the huge parabasal, a dermal bone nearly covering the roof of the mouth, anterior and lateral to which are seen the dentigerous premaxillaries, vomers, and palato-pterygoids. The paraquadrates form a part of the outer margin and a conspicuous process from them is attached to a similar process that projects from a very small oval bone, the operculum, which closes the opening into the otic capsule. The same four cartilage bones seen from the dorsal side appear here, three of which strengthen the otic region while the fourth forms the suspensorium for the attachment of the mandible.

The Chondrocranium.

If, now, as may be easily accomplished in a macerated skull, the dermal or "shingle" bones be carefully removed, there remains a very curious piece of cartilage suggestive of an inner framework, the primordial skull, or chondrocranium. The cartilage bones, previously noticed and now entirely uncovered, are very evidently the result of localized processes of ossification within this, which have taken place in what was once a continuous cartilaginous mass, the homologue of the wholly cartilaginous skull of the present Selachians.

The chondrocranium consists essentially of a delicate framework which runs around the entire cranial cavity and with which certain other cartilaginous elements are associated in varying degrees of intimacy of relation. The framework consists in the embryo of a pair of lateral bars, placed parallel to one another and divisible into an anterior element, the trabecula, and a posterior, or parachordal element. In the adult these names are retained as designations for the regions corresponding to those elements, the trabecular region being that anterior to the otic capsules, while the part associated directly with the capsules themselves is the parachordal region. Posteriorly, between the otic capsules the frame is completed by a pair of cartilaginous bands or arches, of which one, the supra-occipital arch,[1] passes dorsal to the nerve cord, and the other, the basi-occipital arch, lies ventral to this latter part. According to Miss Platt, the supra-occipital arch is really the neural arch of a vertebra anterior to the atlas, which has fused with the skull to increase its strength. At the anterior end of the skull the frame is completed by the development of an internasal plate which connects the convergent trabeculae. Anterior to this the free ends of the trabeculae are continued a short distance in the form of small rostral processes.

Of the originally external elements, the two large otic capsules are the most intimately related and are completely fused with the posterior portion of the primary part and thus form the largest and most voluminous portion of the chondrocranium. Anterior to these are the semi-detached quadrate cartilages, connected with the sides of the trabecular frame by a narrow process, the trabeculo-quadrate isthmus. Still farther forward and separated from the latter by an interval in which are situated the eye and its accessory organs, appears a pair of distinct cartilages, attached to the trabeculae by connective tissue. These are the ante-orbital processes plainly representing a rudiment of the subocular arch, or pterygo-quadrate process, so enormously developed in the frog and other Anura, an homology suggested by W. K. Parker's term of "ethmo-palatine process."

The other cartilaginous parts topographically associated with the chondrocranium are the nasal and optic capsules, of which the former lies directly upon the anterior end of the completed skull, and barely comes in contact with the chondrocranium, while the latter is completely isolated. These parts will receive separate treatment later.

The ossifications of the chondrocranium (= "cartilage bones") are few in number in comparison with those of most Urodeles and consist of but four pairs: (1) the quadrates, used to form a strong support for the mandible, (2) the exoccipitals, forming the condyles

[1] Miss Platt objects to the term "occipitale superius" for the dorsal cartilaginous arch on the ground that the supra-occipital is not an amphibian bone and prefers "interoccipitale," as suggested to her by Gaupp. This term, however, leaves out of account the ventral arch, unless we use the terms "interoccipitale dorsale" and "interoccipitale ventrale" which are cumbersome and possess the disadvantage of the substitution of new terms for old and readily understood ones. Moreover, a portion of the Amniote supra-occipital is preformed in cartilage, and it seems more than probable that there is at least a partial homology between it and the cartilaginous arch found here. The same may also be said of the basi-occipital piece.

and thus strengthening the important articulation of the head with the vertebral column, and (3 and 4) two ossifications of the otic capsule. These, of which the anterior is the pro-otic, and the posterior the epi- and opisthotic combined, are in the form of hollow cups which fit over the anterior and posterior ends of the otic capsule, looking, to borrow W. K. Parker's vivid simile (in Proteus), "as if they were ready to dehisce transversely like the pyxidium of the pimpernel (Anagallis)."

The Osseous Elements.

The otic and occipital regions.— 1. PRO-OTIC. This very irregular bone consists essentially of a conical cap to which are added four projecting processes, one upon the inner and three upon the outer aspect. The inner process, the ala, is flat and wing-like and is applied along the outer edge of the base of the trabecula. Of the three processes which project from the external face of the bone, the two anterior ones, dorsal and ventral quadrate processes, possess concave and roughened articular surfaces to receive corresponding processes of the quadrate cartilage. The ventral process may be considered an extension of the ala, and it receives a rounded protuberance situated in the middle of the posterior margin of the cartilaginous quadrate. The dorsal quadrate process forms the external dorsal edge of the bone and displays a more elongated articular surface for the reception of the otic process of the quadrate. The remaining external process has no relation with other skeletal parts and its probable use is that of attachment for some important muscle or ligament, as it is very constant in appearance and always well

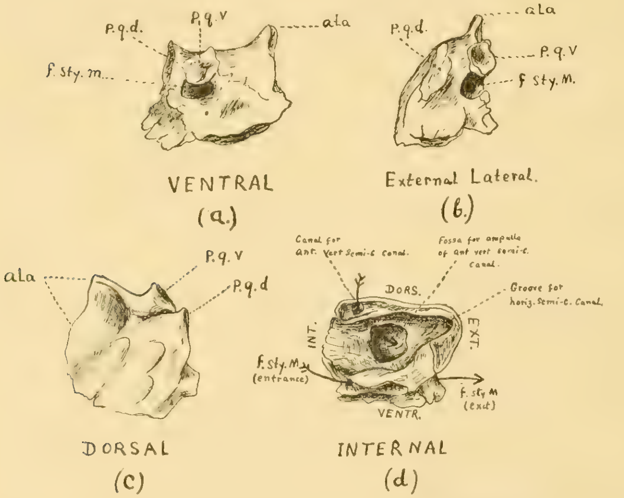

Fig. 8. Four views of the right pro-otic. p. q. d., dorsal quadrate process; p. q. v., ventral quadrate process; f. sty. m., stylo-mastoid foramen.

developed, but this point must be left for later investigation. It runs parallel to and very near the ventral quadrate process, and between the two there is thus formed a deep notch, at the bottom of which is seen the outer opening of the stylo-mastoid canal, that transmits the facialis nerve. This canal enters the pro-otic at its inner posterior margin, traverses almost its entire ventral wall and emerges by the notch just described.

Internally the pro-otic is hollowed out for the reception of the anterior portion of the membranous labyrinth. At the junction of its internal and dorsal edges there is a canal for the transmission of the anterior vertical semi-circular canal, the ampulla of which lies in a deep but narrow excavation at the apex of the cone. The anterior portion of the horizontal semi-circular canal is lodged in a groove upon the outer side of the internal excavation, just beneath the dorsal quadrate process.

The pro-otic may come in contact with three bones, the actual condition varying with the age and degree of development. Its ventral surface is always overlapped by the parabasal, and is usually somewhat roughened over the region of contact. The parietal partly overlaps it dorsally. In large and mature specimens the anterior border of the operculum may touch it upon the ventral side.

2. OPISTHOTIC. This bone consists of a hollow cup, forming the posterior lateral angle of the skull, and investing the posterior part of the otic capsule. It is irregularly conical in shape, being somewhat flattened like a triangular pyramid, and thus presents externally for examination three nearly flat surfaces, a dorsal, a ventral, and an internal lateral, facing the occipital condyle. Of these surfaces, the dorsal is the flattest, the ventral is quite convex, and the internal lateral is marked by a deep groove along which lies the vagus group of cranial nerves. The apex of the cone or pyramid is directed backwards and a little outwards, and terminates in a slightly elevated process, which may be called the mastoid for convenience, since it has some analogy with the mammalian process of that name.

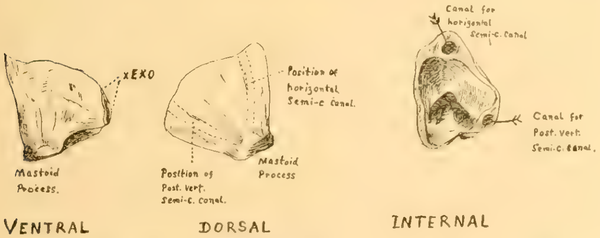

Fig. 9. Three views of the right opisthotic. × 3. Taken from a specimen smaller than in the case above.

Internally the bone presents two canals, a large central depression, and in the bottom of the latter a still deeper recess into which the canals open. The two bony canals, which are excavated in the dorsal wall of the hollow cone, may be distinguished as the lateral

and median, and lodge, respectively, the horizontal and posterior vertical semi-circular canals of the membranous labyrinth. The ampullae of these two canals lie at their posterior union and are situated in the deep recess. The large central depression forms a portion of the median chamber which contains the membranous vestibule with its large otolith. The opisthotic comes in contact with two bones, the paraquadrate and the exoccipital. The former merely overlaps with its posterior portion the outer margin of the opisthotic, but the exoccipital forms, at least in large specimens, a definite union through the medium of distinct processes projecting from the two bones.

The side to which a given opisthotic bone belongs is best determined by the canals and the deepest recess. The canals lie nearest to the dorsal surface and the recess is on the internal side.

3. EXOCCIPITAL. This pair of bones, the bodies of which form the occipital condyles, embraces and defines the foramen magnum and, with the addition of dorsal and ventral cartilaginous arches, entirely encloses it. Each bone consists of a body and two flat processes, the supra- and basi-occipital alae. The body is practically identical with the condyle, and its posterior aspect forms a rounded surface for articulation with the atlas. The dorsal or supra-occipital ala is nearly perpendicular to the rest of the bone and to the floor of the skull and is set obliquely, at an angle o about 45° with both longitudinal and transverse axes of the head, so that, when viewed from above, the median occipital region forms a conspicuous re-entrant angle. This ala arises from the body as a narrow stalk which rapidly widens, and thus resembles a triangle resting upon its apex. The dorsal margin, or base of the triangle, is grooved for the reception of the cartilaginous arcus supra-occipitalis which spans the median interval between this ala and its opposite.

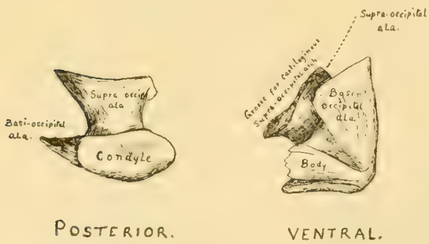

Fig. 10. Two views of the right exoccipital. × 3.

The ventral or basi-occipital ala lies exactly in the horizontal plane, coincident with that of the parabasale, and is applied so closely to this latter bone by its ventral surface that the separation is often attended with some little difficulty. Both W. K. Parker and Wiedersheim found the exoccipitals in Proteus actually a part of the parabasal, or, as the latter expresses it, "synostotisch verbunden." This is nearly the case in Necturus, but, as the two bones are really separable in all cases tried, it is possible that this may be the actual condition in Proteus also. The ventral ala is triangular in shape but is attached to the body of the bone by a side and not an angle, and, when viewed from the ventral side,

forms with the condyle a right-angled triangle, the right angle facing the middle line and the hypothenuse forming the lateral side. The small interval formed between the opposing right angles of the two exoccipitals is spanned by a ventral cartilaginous arch, the arcus basi-occipitalis, which, with the supra-occipital arch and the two bones under consideration, completes the enclosure of the foramen magnum.

This basi-occipital cartilage is of greater extent in young and larval animals, and the ventral alae result from the gradually increasing ossification of its lateral ends. As this process continues towards the center, the inner angles of the bone nearly touch one another in old adults, while the cartilaginous arch is correspondingly diminished.

The exoccipital comes into contact with four bones: (1) the parabasale, which is closely applied to the basi-occipital ala, (2) the opisthotic, which, in adults, touches both the body and the dorsal margin of the supra-occipital ala, (3) the parietal, a bit of the posterior margin of which becomes applied to a corresponding portion of the dorsal margin of the supra-occipital ala, within its contact with the opisthotic, and (4) the atlas, which articulates with the condyles by a movable joint.

The natural relations of an isolated exoccipital are best learned from the flat ventral surface. The condyle is posterior and the long straight edge is internal.

4. QUADRATUM. This is primarily a cartilaginous element, associated with the primordial skull, and representing the proximal (posterior) end of the palato-pterygo-quadrate arch, the functional upper jaw of the Selachians. In the Anura this arch is entire, but in Necturus it is represented by its two ends alone: the antorbital process, which represents its anterior, and the quadratum, its posterior portion.

Functionally it serves as a "suspensorium," or piece interposed between the skull and the mandible, and forming an articular surface for the latter. This joint occurs at its outer anterior angle, and that region of the quadrate becomes ossified, plainly to give strength to this very important joint. It thus happens that there is in the adult, both an osseous and a cartilaginous quadrate, the former being situated externally and the latter towards the median line.

The irregular shape of the quadrate taken as a whole may best be seen by a reference to figures 10 and 11 (plate 64). The external osseous portion consists of an anterior articular process of very hard bone, fitted with an articular socket to receive the rounded cartilaginous knob (articulare) of the mandible, and a hollow trough-like posterior process fitted over the outer edge of the cartilage much as in the case of many of the dermal bones. The cartilaginous portion consists of a flattened plate which attaches by its broadest side to the bony portion and tapers down to a narrow isthmus as it approaches the skull. Contact with the latter is formed by means of anterior and posterior extensions of the isthmus, which become applied to the outer side of the trabecula just in front of the

otic capsule. It is difficult to determine, in a piece of this shape, the location of the processes cited by authors in their description of the quadrate of other Amphibia. The posterior lateral extension which runs along the side of the bone is probably the otic process, and the narrowed part, or its posterior prolongation, the pedicel. Of the two processes which form the isthmus and become applied to the trabecula, the anterior one may possibly be the ascending process. A slight angle seen in the anterior margin is doubtless the rudiment of the "cartilaginous pterygoid" found in most Urodeles, the extension of which to the antorbital process would form the palato-pterygoid arch which is wanting here. Aside from its attachment to the trabecula, the quadrate, osseous and cartilaginous, enters into more or less complete attachment to four bones. As described above, two processes of the pro-otic form quite definite articulations with the quadrate cartilage, the ventral one receiving an articular surface formed by a thickened piece of cartilage in the middle of the posterior margin, and the dorsal one being applied along the inner edge of the otic process. The paraquadrate overlaps it externally, and the outer posterior corner of the palato-pterygoid fits into a groove in the inner side of the articular process and overlaps a raised area of the quadrate cartilage. The cartilaginous articulare of the mandible forms a movable articulation with it.

In determining the position of an isolated osseous quadrate it may be remembered that the side showing the hollow groove is internal, that the larger end is anterior, and that the broader, plainer surface is dorsal.

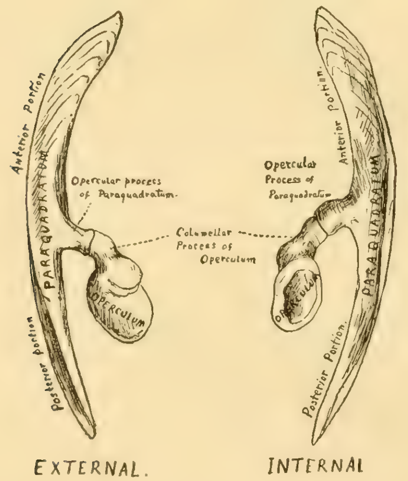

Fig. 11. Right paraquadratum and operculum. Two views. × 3.

5 and 6. PARAQUADRATUM AND OPERCULUM. These elements, of which the first is a dermal bone, and the second an ossification of a detached portion of the otic capsule, are closely connected topographically and joined to one another by strong ligament which unites processes in each bone mutually directed toward the other. The paraquadratum, the shape of which suggested a boomerang to Huxley, attached in its normal manner to the little discoidal operculum, presents the appearance given in figure 11. When in place upon the skull, the paraquadrate lies along the outer side of the otic region, forming the two sides of the pentagonal outline of the skull designated above as "paraquad-

rate," while the operculum fits tightly and exactly into the fenestra ovalis, a large lateral opening in the cartilaginous otic capsule.

The most conspicuous character of the paraquadrate is the short and blunt opercular process, which projects from the inner edge of the curved bone at approximately the middle and thus divides it into two nearly equal portions, the anterior or quadrate, and the posterior, or opisthotic halves. These two halves are nearly flat, or like very shallow troughs, the planes of which are set nearly at right angles to one another; and when in place, the anterior portion is placed nearly perpendicularly to the skull overlapping the quadratum along the side, while the posterior portion is nearly horizontal and covers the outer part of the dorsal surface of the opisthotic.

The paraquadrate is always connected with three bones and may possibly come in contact with two more. By its opercular process it forms a definite articulation with the columellar process of the operculum, and its two flat portions are applied to the outer surface of the quadrate and opisthotic. Aside from these, its anterior and posterior ends may touch the outer corners of the palato-pterygoid and parietal respectively. If an isolated paraquadrate be held so that the opercular process is directed downwards, it is in its normal position and the position of the planes of the anterior and posterior portions will serve to locate it.

The operculum fits something like a stove lid into the fenestra ovalis, an oval opening in the cartilaginous otic capsule. It consists of a flattened oval base or body bearing upon its outer surface an irregular columellar process. By means of this process it articulates with the opercular process of the paraquadrate and normally touches no other bone, although in old animals the pro-otic bone may enlarge sufficiently to come in contact with its anterior edge. The columellar process is directed upwards and a little forwards, and will thus give the proper orientation for the bone.

The homologies and, consequently, the nomenclature of these two bones have been a matter of much uncertainty and varient treatment among authors. For the first of these I have selected the term "paraquadratum" on the authority of Gaupp, who has proposed it as at least a provisional term to indicate the dermal encasing piece associated in the amphibians with the quadrate. He apparently inclines to the belief that this element may prove homologous with the mammalian tympanicum, a term by which he designates the piece in his revision of the "Anatomie des Frosches." The operculum has become so universally identified with the stapes of higher forms that in the first writing of the manuscript for this work the word "stapes" was used and its probable homology stated. I was led to a change of this view by the examination of a set of slides of a larval Necturus of 44 mm. in which the part in question arises as a semi-detached bit of the cartilaginous otic capsule, precisely as was seen by Stöhr in Triton and Siredon. This was equally

evident and presented a similar appearance in a series taken from a larva of 26 mm. This observation, which seems perfectly clear and unassailable, and which corroborates the results given by Stöhr in other Urodeles, is absolutely at variance with the statement of Miss Platt, who says that "it arises independently" and identifies as its anlage a mass of cells which, in an embryo of 19 mm., is situated just in front (outside) of the fenestra ovalis, and between it and the end of the ceratohyal. It is possible that this anlage may represent a true columella or hyomandibular cartilage, which may later become fused with the true operculum to form its projecting external process, although in the larvae of 26 mm. and 44 mm., the series which I have examined, I can find no trace of such a double origin of the parts in question.

The brain case.—This is formed in great part by five dermal bones, the two frontals, two parietals, and the parabasale, of which the first four form its dorsal, lateral, and anterior walls, and the parabasale its floor. The box formed by these is deficient posteriorly, where it is completed by the otic capsules and other cartilaginous elements with their ossified areas. Above, each frontal is so completely welded to its accompanying parietal by means of interlocking splints that they practically form one bone while the two sets of united pairs meet in the median line by means of somewhat thickened flat edges, forming symphyses. Upon the ventral surface of this roof, both bones end down extensive processes that lie just within the trabecular arch of the primordial skull and make an extensive ridge in the form of a long narrow U, the loop being directed anteriorly. This ridge forms the front and sides of the brain case and at its ventral edge is everywhere in contact with the parabasale.

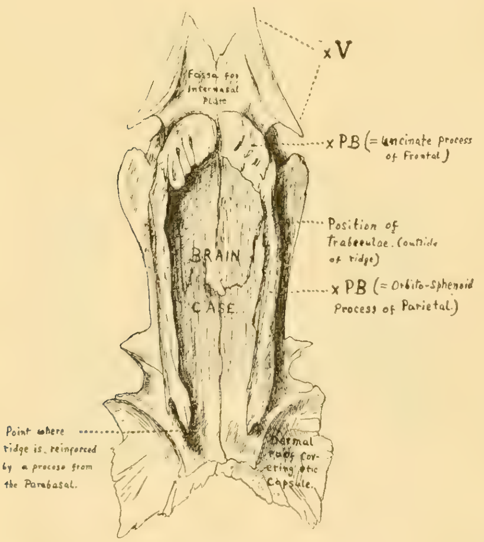

Fig. 12. The roof of the brain case seen from beneath. × 3. This is composed of the two frontals and the two parietals, upon the ventral side of which is developed a series of processes which together form a U-shaped ridge that forms a front and sides to the case. Contact surfaces for other bones are designated by an x and the abbreviations of the bone involved.

The result of this singular formation is that in Necturus the lateral walls of the brain case are formed of solid dermal bone reinforced externally by cartilage while in most Uro-

deles the walls are formed by the cartilaginous trabeculae or in part by an ossification in these elements, the orbito-sphenoid. A foramen for the olfactory nerve is formed at the junction of the frontal and parietal contributions to this ridge; other nerves, as the trigeminus and facialis, emerge from the cranial cavity just posterior to it, but the nerves to the eye muscles and the opticus pass through tiny foramina, running very obliquely through the process itself.

The floor of the brain case is formed by the very extensive parabasal, which receives upon its dorsal surface the lateral processes projecting from the roof, and reinforces them posteriorly by a low ridge topographically continuous with them. The details of the separate bones are as follows: —

1. FRONTAL. The frontals form a little more than a third of the dorsal surface of the skull. They lie in contact with one another for about two thirds of their length, diverging anteriorly to form a pair of short premaxillary processes, and posteriorly to form the longer and thinner parietal processes. A single frontal, isolated from its surroundings, resembles a flat and quite irregular splinter of bone from the under (ventral) side of which hangs a partially detached plate directed backwards, the processus uncinatus of Wiedersheim, which forms the anterior portion of the U-shaped ridge described above. The notch enclosed between this process and the main body of the bone transmits the olfactory nerve and is converted into a foramen by the addition of the antero-lateral process of the parietal and the trabecula. A conspicuous process upon the outer margin of the bone in this region, directed backwards, and seeming to belong to the uncinate process rather than to the main body of the frontal, assists also in the formation of the olfactory foramen and may be termed the olfactory process.

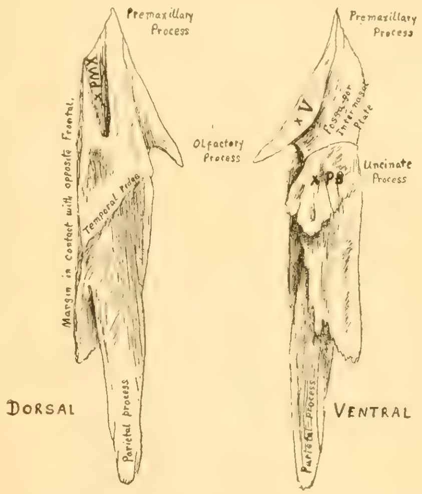

Fig. 13. Two views of right frontal. × 3. Contact surfaces with other bones are designated by an x.

Upon the ventral side of the bone are seen two roughened ridges for the attachment of other bones. Of these the more anterior is a curved ridge connecting the olfactory and premaxillary processes and serving for the attachment of the vomer; the other involves the ventral surface of the uncinate process and comes in contact with the parabasal.

Between them is a flattened depression, the internasal fossa, which lodges the internasal plate of the chondrocranium. The dorsal side possesses few features of interest. At the anterior end is a longitudinal groove in which rests the ascending process of the premaxillary and farther back is an oblique temporal ridge, extending from the olfactory notch to the middle of the interfrontal suture, and serving as the anterior limit of the temporalis muscle.

2. PARIETAL. This is the most irregular bone of the skull, and the largest, with the exception of the parabasal. It possesses extensions in several directions, but it is so irregular that the number of definite processes, of which Wiedersheim enumerates five, is somewhat arbitrary. Of these, the most important functionally as well as anatomically, is the longitudinal ridge upon the ventral side, the edge of which comes in contact with the parabasal, and which functionally replaces an orbito-sphenoid and serves as the side of the brain case. This may be called the orbito-sphenoid process, as suggestive of its function, and this process together with the uncinate process on the frontals completes the U-shaped ridge mentioned above. This ridge is perforated by several very slanting foramina for the transmission of the nerves of the eye muscles, but the exact identification of these must be left for later investigation. The irregularly curved and very thin dorsal surface may be conveniently divided into a nearly flat anterior portion and a decidedly convex posterior portion, taking its shape from the otic capsule which it covers. From the anterior portion proceed three processes, an antero-median, an antero-lateral, and a quad-

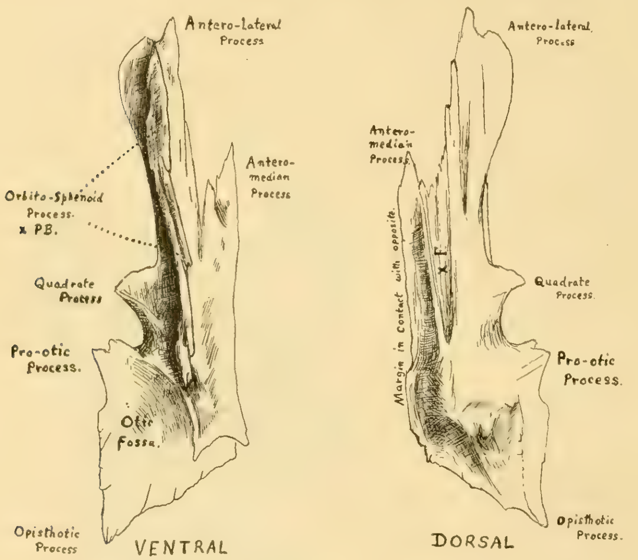

Fig. 14. Two views of right parietal. × 3. Contact surfaces with other bones are designated by an x.

rate. The first two receive between them the parietal process of the frontal, and the antero-lateral one, which is much the larger, reaches the olfactory region and assists in the formation of the olfactory foramen. This process bears upon its ventral side a large portion of the orbito-sphenoid process. The quadrate process is small and flat, and projects over that part of the quadrate cartilage designated above as the "isthmus." The outline of the posterior portion is practically a square, of which the two outer corners are obvious, the posterior one being considerably prolonged. These may be termed respectively the pro-otic and opisthotic processes in reference to the bones which they partially overlap. This portion forms a thin outer covering for the otic capsule and corresponds to it in shape, being convex above and concave beneath. It forms the otic fossa of the ventral surface.

There are several prominent muscular ridges upon the dorsal surface of the parietal, the most important of which are several irregular ones upon the posterior portion and a median one formed between the two bones and prolonged into a median intermuscular septum.

3. PARABASAL. This is the flattest and most extensive bone of the skull and forms nearly the whole of the floor of the brain case, and at the same time the roof of the mouth. It is nearly in the shape of a parallelogram with rounded corners, but is a little broader in the otic region and becomes somewhat narrowed anteriorly. It is almost without special features other than the impressions made by the bones which come in contact with it, the frontals and parietals upon its dorsal, and the vomers upon its ventral surface. Upon the dorsal surface at the posterior end there is a pair of low lateral ridges which reinforce the orbito-sphenoid processes of the parietal and

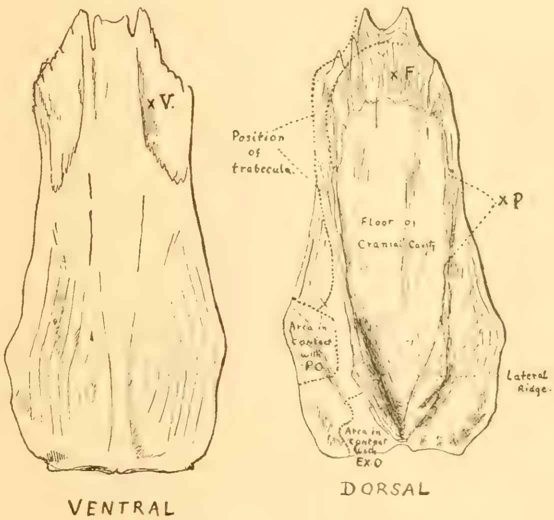

Fig. 15. Two views of the parabasal taken from different individuals. The view of the dorsal side is 4 times enlarged, that of the ventral, being from a much larger individual, but 2½. Contact surfaces with other bones are designated by an x.

converge at the posterior end. There is necessarily a slight depression between them, but anything as marked as the depression described by Wiedersheim and likened to a "sella turcica," I have failed to find. Probably this outline would be much more noticeable in cross sections, which were studied extensively by this author, and in a young animal it is likely that it would be proportionally more marked. The parabasal normally comes into contact with ten bones, eight upon the dorsal surface and two upon the ventral. Dorsally there are found in order, the two frontals, and the two parietals, by their uncinate and orbito-sphenoid processes respectively; the two pro-otics, and the two exoccipitals, the latter almost anchylosed with it in old adults. Upon the ventral side are the two vomers. The palato-pterygoids and the opisthotics come very near the parabasal, but form no definite area of contact.

The upper jaw.— Under this term may be included all the dentigerous bones of the skull proper, as the teeth of all these oppose those upon the mandible. In this group both of the typical arches are represented, the maxillary and the palato-quadrate, or the "inner" and "outer arches" of W. K. Parker, the former by the premaxillaries and the latter by the vomers and palato-pterygoids. Each of these arches bears a row of teeth, and, when the mouth is closed, the single row on the mandible is received between the two upper rows. The internal or palatine row is longer than the external or maxillary.

1. THE MAXILLARY ARCH. This arch is represented in most Urodeles by both premaxillaries and maxillaries, the latter extensive and ending in long, backward projecting processes which, in the recent state, are attached by strong ligaments to the quadrates, thus making the arch a complete one. In Necturus it suffers much reduction and is represented by the premaxillaries alone. The maxillary fails completely, and no rudiment of it seems to be present at any developmental stage. Hyrtl describes a dried specimen with a small but tooth-bearing maxillary upon one side. Neither Huxley nor Wiedersheim could find a trace of it, and in an examination of more than fifty skulls I have never seen it. The specimen described by Hyrtl must have been either an abnormal case or one of mistaken identity.

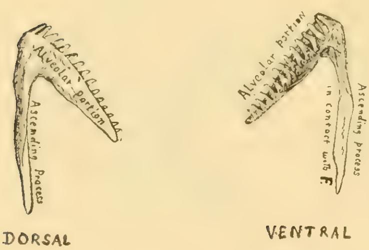

Fig. 16. Two views of right premaxillary. × 3.

a. Premaxillary.— This bone consists of a slightly curved alveolar portion, to the inner end of which an ascending process is added at nearly a right angle. The alveolar portion is placed in an antero-lateral position, ventral to the large nasal capsule, which lies obliquely across it and forms the anterior part of the outer margin of the skull. The ascending

process is in the form of a flattened splint and is superposed upon the dorsal surface of the anterior end of the frontal, lying in a shallow groove formed for its reception. This is the only contact between the premaxillary and any of the other bones of the skull; but the extreme tips of the rostral cartilages may touch its ventral surface, and the two premaxillaries almost touch each other at their antero-internal angles.

2. THE PALATO-PTERYGOID ARCH. This arch in Urodeles consists typically of three dermal elements, vomer, palatine, and pterygoid, but owing to fusion or loss of one or more of the elements, it usually appears in a modified form. In some Urodeles the first two of the typical elements fuse and form a broad vomero-palatine, while in others, as is the case in Necturus, the vomer is distinct and the second and third elements fuse to form a palato-pterygoid. Usually in the vicinity of the pterygoid there is a part of the primitive cartilaginous palato-pterygoid arch around which the dermal bones may be supposed to have originated, and this is denominated the "cartilaginous pterygoid." In a few cases (Desmognathus, Batrachoseps) the osseous pterygoid fails, leaving the vomero-palatine as the sole dermal representative of the arch.

a. Vomer.— The main portion of this bone is somewhat triangular in shape and forms the extensive, flattened palatine portion. Added to this upon its outer border appears the alveolar portion, set at right angles to the main part and slightly curved. The palatine portion forms the greater part of the anterior third of the roof of the mouth but the two bones do not meet in the middle line. The inner borders, forming the longest side of the triangle, are quite near one another anteriorly but diverge posteriorly, and in the space thus left appears the parabasale, which also extends along the dorsal side of the palatine process of the vomer, thus doubling the bony roof of the palate over a large extent of the anterior surface. The parabasal does not, however, extend anteriorly as far as the vomerine teeth, and there is thus left a considerable interval, bounded by the above mentioned teeth, the inner borders of the vomers, and the anterior border of the parabasal, where there is no bony roof. This opening is nearly square, and through it, in the prepared skull, there may be

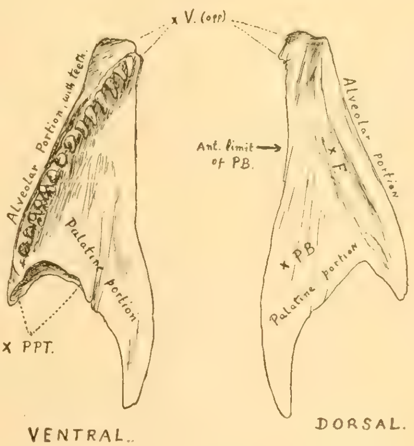

Fig. 17. Two views of right vomer. × 3. Contact surfaces with other bones are designated by an x.

seen the internasal plate of the primordial skull. Viewed from the ventral side, the two vomers may be said to overlap the parabasal, and the areas of contact are clearly marked upon the dorsal surface of the former bone and the ventral surface of the latter. The frontal bone comes in contact with the vomers dorsally, and the articular surface for this forms a long, narrow ridge, running along the lateral border above the row of teeth. At the extreme anterior end, the two vomers come in contact with each other, the symphysis being marked by a few jagged, irregular projections. The postero-lateral border of the palatine portion is recurved and exhibits an articular surface for the anterior end of the palato-pterygoid.

b. Palato-pterygoid. — This is a flattened bone, somewhat in the form of a narrow parallelogram, but with the anterior end rounded. It is set in the skull obliquely to the longitudinal axis and extends from the vomer to the quadrate, articulating with both and with no other bones. Its alveolar portion is small and confined to a short curved ridge upon the outer border at the anterior end. The space between the inner border of this bone and the outer border of the parabasal is in the form of a very narrow triangle and is filled in the recent state by a firm membrane. The orientation of this bone may be easily made by the teeth which are upon the ventral side, at the anterior end, and along the outer margin.

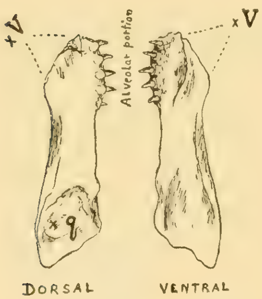

Fig. 18. Two views of right palato-pterygoideum. × 4, (from small specimen). Contact surfaces with other bones are designated by an x.

The Visceral Skeleton.

General morphology of the arches.— The seven visceral arches inherited from the Selachians, and surviving in most higher vertebrates, are represented here, although one of them (the 6th) is vestigial, and appears in the adult as merely an intermuscular septum. Their disposition is as follows: —

1. This arch, forming the functional jaws of the Selachians, possesses typically a dorsal and a ventral segment, of which the former is represented by the cartilaginous palato-quadrate arch, and the latter by Meckel's cartilage of the mandible. Both of these arches, in most higher vertebrates, become encased by dermal bones and lose their identity more or less completely in the adult, the palato-quadrate arch suffering more in this particular than the other. In Necturus the anterior and posterior ends of the palato-quadrate arch survive as the antorbital process and the quadrate cartilage (including its ossification) respectively, and the median portion is unrepresented. The

dermal bones connected with this arch are the vomer and the palato-pterygoid. These as well as the quadrate have been previously described. The ventral segment is represented by a very complete pair of Meckel's cartilages, encased by three dermal bones, the dentale (dentary), spleniale (operculum), and angulare. The proximal, or posterior end of this cartilage forms a rounded articular surface which articulates with the mandibular process of the quadrate, and forms an element often ossified in amphibians, and then known as the articulare.

2. The second visceral arch consists in the Selachians of a dorsal segment, the hyomandibular, and a ventral segment, the true hyoid. The latter piece is always present and well developed in Urodeles, and in Necturus consists of two well developed cartilages upon each side, but opinions differ widely concerning the fate of the hyomandibular. The views which connect it with the stapes of mammals and the columella of reptiles seem to have much support, but any connection between it and the Urodele operculum is evidently disproven by the origin of this latter piece from the side of the otic capsule. It thus seems safe to assert that the dorsal or hyomandibular segment of the second visceral arch has no skeletal representative in Necturus.

3–5. These are the three gill arches which guard and regulate the two gill slits situated between them upon either side of the neck, support the three pairs of integumental branchiae, and furnish attachment for the muscles which regulate them. This association of external branchiae, belonging to the integumental system, with the three gill arches, which in fishes support the internal endodermic gills, has led in the past to a confused suggestion of homology between these genetically distinct structures. The gill arches are represented here by twelve cartilages, five on each side and two in the median line, and all of these pieces are joined with the four of the hyoid arch to form the hyobranchial apparatus.

6. This is the rudiment mentioned above, and represented by an intermuscular septum.

7. This arch is represented by a single pair of cartilages which guard the entrance to the trachea and extend along its sides; the cartilagines laterales, or laryngo-tracheal cartilages.

The parts will now be taken up in detail.

The mandible.—The mandible consists of the four separate elements mentioned above: Meckel's cartilage and the three dermal bones, dentale, spleniale, and angulare. The cartilage is well encased by the dermal pieces, but its surface is exposed along a part of the internal aspect, as well as over a large portion of the proximal, or articular end, where it forms the joint. In the larva the cartilages of the two sides meet at the mid-ventral line, and receive the protection of the dentalia upon their outer side alone, but as

these latter bones develop, they expand somewhat at their meeting with one another and form a strong bony symphysis, suppressing the median ends of the cartilage. The dentale is the largest of the dermal bones and covers the entire outer side of the mandible from symphysis to posterior angle. It forms nearly the anterior third of the inner surface, and two thirds of the lower edge, forming, with the lower border of the angulare, the foramen mandibulare. The angulare is next in size and is the main bone of the inner surface, extending along the posterior two thirds of the mandible. It forms the posteriorly directed angular process, and a small part of the bone appears in this region upon the outer surface. The spleniale is very much reduced in Necturus and is in the form of a little oval scale, set somewhat on the inner side, filling an interval between the angulare and the dentale. It is dentigerous and bears a few (5 to 7) teeth, which form a row not exactly continuous with that of the dentale, and opposed to that of the palato-pterygoid in the upper jaw. The details of the above osseous elements follow.

1. DENTALE. This bone gives the contour to the jaw and follows quite closely the general outlines of the head, and thus the posterior part is nearly straight while the anterior third curves somewhat abruptly inwards. It is quite thin and its upper and lower edges are curved inwards, making its outer surface somewhat convex and the inner con-

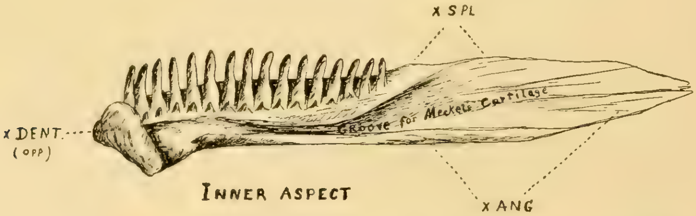

Fig. 19. Internal view of right dentale. × 3. Contact surfaces with other bones are designated by an x.

cave. At the anterior third so much of the lower edge curves in that it forms a fairly broad and flat submental surface involving about half of the total width. The dentale bears a row of teeth which occupy nearly the anterior half. They are inserted along the inner aspect, about half their length appearing above the upper edge of the bone. Just posterior to this row of teeth the upper margin rises a little to form a very rudimentary ramus which receives the insertion of the very stout tendon of the masseter muscle. Internally, the dentale is chiefly characterized by its concavity, which lodges Meckel's cartilage and forms a deep and narrow groove anteriorly which broadens out posteriorly to the full width of the bone.

The two dentalia form a strong symphysial articulation with one another at their

anterior ends, a union which, in a macerated skull, often holds long after the separation of the other components of the jaw. The recurved ventral margin of the dentale becomes closely applied upon the inner side of the mandible to the corresponding edge of the angulare and usually completes the formation of the intermandibular foramen. The spleniale comes in contact with it by a portion of its outer surface.

2. ANGULARE. This bone is a curved splint, broad behind and tapering anteriorly into an extremely fine and sharp point. Its outer aspect is concaved to receive Meckel's cartilage, and this surface, together with the inner surface of the dentale, forms a nearly complete canal for the protection of the cartilage just named. The most solid portion of the bone is that which forms its lower margin, and this part, when articulated with the dentale, forms a direct continuation of the flat submental surface of the latter. Posteriorly it ends in a blunt, rounded, angular process which furnishes attachment to the digastric muscle. Along the external aspect of this heavy portion there run a sharp edge for articulation with the ventral edge of the dentale, and in this, at about its posterior third, is either a deep notch or a complete foramen, the former being much the more usual. This is reinforced by the edge of the dentale and forms the mandibular foramen, through which the mylo-hyoid branch of the fifth nerve reaches the intermandibular region. The remaining, or dorsal part of the bone forms a flattened and much curved wing ending in a sharp upper edge, the rounding outline of which forms a coronoid process which receives the insertion of the temporalis muscle. Along the anterior slope of this process the upper margin is applied to the lower margin of the spleniale.

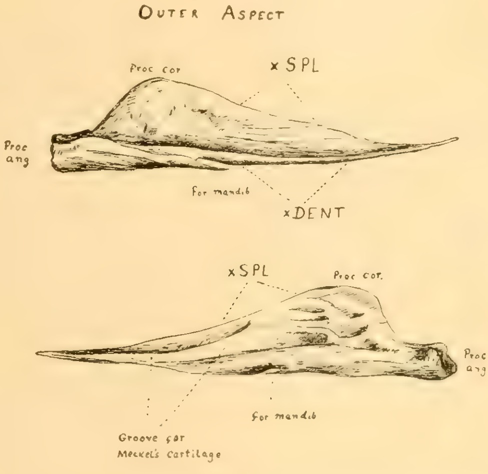

Fig. 20. Two views of right angulare. × 3. Contact surfaces with other bones are designated by an x.

This bone is easily oriented, since the more solid base is ventral and the slight curve of the main axis follows the curve of the jaw.

3. SPLENIALE. Next to the operculum of the otic capsule, this is the smallest bone of the skull, and by a singular coincidence, many authors have given it the name "oper-

culare," thus producing a confusion of terms. The spleniale is a thin scale of oval shape, presenting a slightly concave inner, and a slightly convex outer surface. Along the side of the former is attached a row of teeth, and the outer surface shows a longitudinal division into an area covered by the dentale and a free area, which contributes a little to the formation of the outer surface of the mandible.

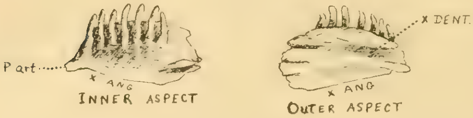

Fig. 21. Two views of right spleniale. × 3. Contact surfaces with other bones are designated by an x. P. ant., processus anterior.

The oval shape and lack of detail of this bone render its orientation difficult, but its outer and inner surfaces are very evident, and in most cases the anterior end is prolonged into a point, while the posterior end is rounded. In its natural position it rests by its lower margin upon the upper edge of the angulare just anterior to the coronoid process, and the ventral half of its outer surface is closely applied to the dentale.

The hyobranchial apparatus. — This consists of a series of sixteen pieces, all but one being entirely cartilaginous, and representing four of the original visceral arches. Their arrangement is so easily seen from plate 65, figure 12, that a verbal description of the parts would seem almost superfluous. The system is seen to contain two median pieces, universally designated as the first and second basibranchials, and referred to the first and second branchial arches respectively, of which they form the middle pieces or copulae. Of these, the second is ossified in the adult and its free posterior end usually terminates in a rounded extremity, although an occasional individual shows a division at the end into a two or three forked form, such as occurs normally in Siren. The hyoid arch, which is attached to the anterior end of the first basibranchial, consists of two pieces, an inner hypohyal and an outer ceratohyal. The first branchial arch is the best developed of all the branchial arches, consisting of two nearly equal pieces, cerato- and epi-branchiale 1, the first of which is directly connected with both the first and second basibranchial and with its opposite. The second branchial arch consists of a smaller epibranchial, and a rudimentary ceratobranchial, reduced to a nodule of cartilage lying upon the inner side of the distal end of the first ceratobranchial. An epibranchial smaller than the previous one is the only remnant of the third branchial arch.

In life the distal ends of the three epibranchials support the external integumental branchiae and furnish attachment for some of their muscles, a circumstance which has often misled investigators as to the true homology of these purely integumental organs, since the location suggests a definite phylogenetic relation to the internal gill system. In the intervals between these epibranchials there occur, even in the adult Necturus, two

open gill slits guarded by rudiments of gill rakers, much as in the Axolotl, and as these occur, the one between the first and the second arches, and the other between the second and the third, and consequently in the intervals between the integumental branchiae, the suggestion of connection between the two systems is still more misleading. It may be remembered in this connection that there is a similar external gill upon the shoulder girdle in the Dipnoan, Protopterus, the relation of the two being wholly topographical and without morphological significance. Hence the physiological moments which have developed the external branchiae in this place are plainly the utilization of the gills and their muscular mechanism for support and motion, as well as the currents of fresh water which can be driven through the gill slits in such a way as to bathe the respiratory fringes.

Since the attempt of Fischer ('64) to account for a fourth branchial arch by supposing that the first consists of two fused arches, no good suggestion concerning branchial arches posterior to the third had been made up to about ten years ago, since when a series of investigations by Gegenbaur (29'), Göppert ('94), and myself ('92), have rendered it probable that the laryngo-tracheal cartilages of Amphibia are modified portions of the fifth arch, perhaps the epibranchials. A fourth arch, attached to the hyobranchial apparatus, is present in several of the lower Urodeles, (Siren, Amphiuma, Cryptobranchus), and its apparent absence in Necturus has awakened some little speculation. The rudiment of this was finally discovered by Göppert, who found it to consist of a raphe of connective tissue, separating two muscles normally belonging to the branchial system, and in which, in the larva, he discovered a few cartilage cells. This view I can corroborate by investigations upon the same point at the same time, and which had led me independently to the same conclusions previous to the appearance of the work of Göppert. This raphe is given in the figure referred to (pl. 65, fig. 12), and there can now be little doubt that it represents the missing fourth epibranchial. Concerning the structure of the metamorphosed fifth branchial arches (laryngo-tracheal cartilages), they consist normally of a single pair of somewhat curved pieces, applied to the sides of the glottis and short trachea, and were first described by Henle under the name of cartilago lateralis. They are individually very variable and often have notches, foramina, or detached pieces, but consist essentially of an anterior flat piece in the form of a triangle, from the posterior internal angle of which depends a curved tracheal process extending posteriorly. A more careful description of these cartilages and figures of several varying forms are given in the author's article on the amphibian larynx ('96).

Suspensorial relations of the hyoid.— The distal end of the ceratohyal enters into a ligamentous connection with various parts of the skull and mandible and thus bears a close relation to the suspensorial apparatus of the mandible, a region which has such an

important morphological bearing that a description of it is worthy of special consideration. Huxley ('**74**) was the first to describe carefully this region in Necturus, and according to this author there are three important ligaments in this region: (1) a mandibulo-hyoid between the angular process of the mandible and the distal end of the ceratohyal; (2) a hyo-suspensorial between this latter point and the quadrate; and (3) a suspensorio-stapedial, from the quadrate to the operculum. A series of dissections of several very large individuals, under the most favorable conditions as to preservation, has led me to modify somewhat the account given by Huxley, and to substitute the interpretation graphically given in the accompanying figure (fig. 22). The distal end of the ceratohyal is traversed by a deep groove in which runs the tendon of the digastric muscle, and which forms an outer and an inner lip. At the posterior end of the inner lip there is developed a rather prominent process. There are two distinct mandibulo-hyoid ligaments, external and internal, the one from the outer lip of the digastric groove to the lower corner of the angular process, and the other from the inner lip of the groove and from its process to the angular process just above the attachment of the other. The hyo-suspensorial ligament is a narrow but very strong and distinct band extending between the middle of the inner lip of the digastric groove and the outer side of the quadrate bone. In spite of repeated careful dissections I could not find any definite "stapedio-suspensorial" ligament, but instead of this a rather soft and somewhat indefinite sheet of connective tissue extending along the entire inner lip of the ceratohyal and attached along a corresponding length of the skull, involving the operculum, a bit of the cartilaginous otic capsule, and a part of the quadrate. At its posterior edge its fibers become stronger and thicker, and thus resemble a hyo-stapedial ligament, but as this part is directly continuous with the remainder of the sheet and is by no means as definite as the other genuine ligaments, it can hardly be described as a definite part. This loose sheet of connective tissue, which, as a matter of fact, adheres very closely to the columellar process of the operculum, is undoubtedly the

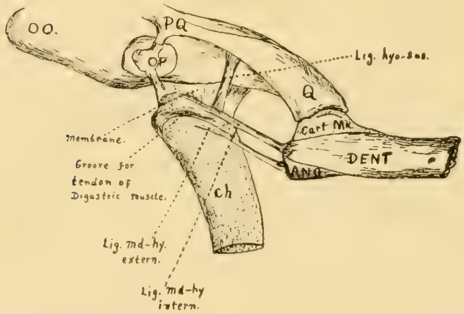

Fig. 22. Relations of suspensorium, jaw and hyoid, taken from the right side. × 3. Lig. hyo-sus., ligamentum hyo-suspensoriale; lig. md.-hy. extern., ligamentum mandibulo-hyoideum externum; lig. md.-hy. intern., ligamentum mandibulo-hyoideum internum; membrane, that between skull and ceratohyal, forming posteriorly a thickened band, extending between operculum and ceratohyal.

part described by Huxley as the stapedio-suspensorial ligament. Certainly no definite ligament, the fibers of which extend between the operculum and the quadrate, can be demonstrated.

In this connection it is interesting to compare the work of other writers on the subject, who have naturally been influenced by the description given by Huxley. W. K. Parker ('77, pl. 28, fig. 5) has figured this region in detail in Proteus. This shows the same broad connective tissue band first described, but no definite stapedio-suspensorial ligament. This band, which appears identical with that which I have described in Necturus, is lettered "st. sl.," but no mention is made of it in the text. The two other ligaments are as in Necturus, if one counts the two mandibulo-hyoid ligaments as one. Wiedersheim ('77) accepts Huxley's statements and quotes them (paraphrased, p. 435). He speaks of a lig. stapedio-suspensoriale in Proteus, but in his figure 19, in which he refers to this ligament as "Prop," he really points out the bony connection between operculum and paraquadratum, showing that he has confused the two, perhaps for the moment. His figure of Proteus is in reality like W. K. Parker's, and well expresses the condition in Necturus.

The Free Sense Capsules.

The nasal capsules and the sclera of the eyes receive a more or less complete reinforcement of cartilage, which is structurally a skeletal part, and may be considered under the heading given above.

The nasal capsules are somewhat in the shape of round-bottom flasks with necks curved outwards, and they lie upon the sides of the anterior angle of the skull, extending from the alveolar processes of the premaxillaries to the antorbital processes. The nostrils or anterior nares appear at the end of the outwardly curved necks and are hence divergent from one another and situated upon the sides of the blunt snout with a wide interspace. The posterior nares lie underneath, near the rounded posterior end, and in close connection with the anterior margin of the antorbital processes which are curved somewhat around them. The sides and roof of each capsule are covered by a delicate reticular or fenestrated cartilage of a soft consistency and rather difficult of demonstration as cartilage.

A very similar structure is found in Proteus, where it was first described by Leydig, in 1853, (quoted by Wiedersheim, '77) and the form in Necturus appears to have been first shown by Wiedersheim, in 1877, who both describes and figures it with great clear-

ness, but may perhaps have given in his drawing somewhat too great regularity to the fenestrations. Both Huxley (Necturus) and W. K. Parker (Proteus) appear to have entirely overlooked the structure or at least not to have recognized its skeletal nature. In the adult it appears like a shell covering the dorsal half of the capsule, its edge being entire and running along the lateral outline. Its surface is perforated by openings in the form of irregular parallelograms approximately arranged in two longitudinal rows and converting the entire structure into a delicate cartilaginous network. At the anterior end a narrow loop appears to extend across the ventral side, thus enclosing the nostril. By an examination of the larvae it would seem that this structure at first consists of a single longitudinal rod applied to the inner side of the capsule, after which transverse rods develop between the folds of the nasal mucous membrane. Miss Platt ('97) has given a brief description of this in a larva of 46 mm., and Winslow ('98) has both described and figured it at the same stage. In the printed description of both authors the transverse lateral processes develop or project directly from the main longitudinal rod, but in Winslow's figure 16 certain of the transverse rods appear entirely separate from the longitudinal one as though they had arisen independently of it. The later development of this capsule and the manner in which the original elements finally weave themselves into the complicated network seen in the adult, are points which have not as yet been investigated.

The term "optic capsule" seems almost too formal a word for the thin cartilaginous ring which appears in the sclera and surrounds the eye. It is hardly demonstrable to the unaided eye but is clearly seen in sections. Miss Platt found it in a larva of 46 mm. to be "three cells wide and one cell deep," and in a small adult, of which I have sections, it is from about 15 to 20 cells wide and about 4 cells deep in the thickest portion, tapering towards each edge. The drawing of it given in plate 64, figure 6, is purely diagrammatic and obtained from sections, as I have not succeeded in preparing an eye so that it could be seen directly. According to Miss Platt, both nasal and optic capsules arise independently.

The Teeth.

The teeth of Necturus are arranged in two parallel rows in the upper jaw and in a single row in the lower, those of the latter fitting into the interval between the two rows of the former, their mutual arrangement being such that the teeth on the dentale oppose those of the vomer, those on the spleniale oppose those on the palato-pterygoid, while the premaxillary teeth form an unbroken outer row shutting over all the rest. At the juncture between the vomerine and palato-pterygoid teeth of the inner, upper row, and again between the dental and splenial teeth of the lower row there are slight breaks in the continuity of the rows, and usually a perceptible diastema or gap. Several of the authors

have given a definite number of teeth for each dentigerous bone, and Cope ('89) has even employed the number of teeth as a diagnostic between species, but as a matter of fact the number is quite inconstant, and it seems probable that the rows are added to upon their outer or posterior ends as the animals become older. The result of a series of enumerations of different specimens may be given in the following tables.

TABLE A.

Teeth enumerated in entire specimens.

Designation of specimen.	Side.	Premaxillary.	Vomer.	Palato-pterygoid.	Dentale.	Spleniale.	Total on a side.	Total teeth.
A	Rt	12	12	5	14	6	49	99
	L	12	13	5	15	5	50	
B	Rt	10	10	5	14	6	45	93
	L	11	11	6	15	5	48	
C	Rt	10	10	5	14	6	45	93
	L	11	11	6	15	5	48	
D	Rt	9	10	6	13	5	43	87
	L	9	11	6	13	5	44	
E	Rt	14	15	8	15	7	59	121
	L	15	15	8	16	8	62	
F	Rt	12	13	8	18	—[1]	—	—
	L	12	12	7	17	—[1]	—	

TABLE B.

Teeth counted in isolated bones.

	PMX.	V.	PPT.	DENT.	SPL.
	14	14	7	20	7
	14	13	8	18	7
	13	13	8	17	7
	15	15	9	16	7
	15	17	8	17	6
		16	6	16	7
		15	6	18	
		17		17	
average [3]	12.5 —	13.0	6.6	15.9 +	6.2 —

[1] These small bones were unfortunately lost in this specimen.

[2] The specimens which furnished these isolated bones were generally larger than those used for Table A, which accounts for the greater number of teeth.

[3] In this average are included the statistics from both tables.

The teeth are pleurodont, *i. e.*, situated upon the inner side of the tooth-bearing ridge, and possess a root and a crown, the division between the two being coincident topographically with the edge of the bone upon the outside of a row of teeth. Thus the root, which is formed simply of bone substance, and is unprotected by enamel, is guarded by the ridge of bone, while the enameled crowns project beyond this protection. The root is made of a hard bony substance or dentine, and is directly continuous with the bone which bears it, arising from it by two lateral supports, which leave between them the characteristic hollow seen in all of the figures that represent teeth as seen from the inner aspect. Each hollow is really a foramen, which forms the entrance to the pulp canal of the crown and serves in life to transmit the special nerves and blood vessels which supply the tooth. The crown is in the shape of a slender cone, with a tip that is often set off a little from the rest by a slight constriction. The apex is pointed and slightly recurved, and is colored at the very point a deep amber color, similar to that found upon the exposed outer surface of the incisors of beavers and many other rodents.

Comparison of Nomenclature.

That the numerous authors who have written upon the Urodele skull have not been in accord with regard to the nomenclature of the elements concerned is to be expected when we consider both the time covered by their investigations, and the fact that grounds for an accurate homologizing of the parts have been sadly lacking, especially previous to the epoch making years of the '60's and '70's. An attempt to arrange the synonyms used by various authors in designating the parts of the skull of Necturus and a few allied forms is given in the following table. The two last columns give respectively the terms used in this work and the abbreviations by which they are designated in the figures.

TABLE C.

Comparison of nomenclature of important parts of the skull.

HYRTL, 1865. (Cryptobranchus)	HUXLEY, 1874.	WIEDERSHEIM, 1877.	W. K. PARKER, 1877. (Proteus)	GAUPP, 1895. (also frog, 1896.)	WILDER, 1903.	Abbreviations.
ossa frontalia[1]	frontal (bones)[1]	frontalia	frontals		frontal	F
ossa parietalia	parietal (bones)	parietalia	parietals		parietal	P
os sphenoideum basilare	parasphenoid	parasphenoid	parasphenoid	parabasale	parabasal	PB
ossaintermaxillaria	premaxillae	premaxillaria	premaxillaries		premaxillary	PMX
os maxillare superius (?)	vomers	vomer[1]	vomers		vomer	V
os pterygoideum [Here without the palatine.]	palato-pterygoid	pterygo-palatinum	pterygo-palatines		palato-pterygoid	PPT
ossa mastoidea	squamosals	tympanicum *sive* squamosum	squamosals	paraquadratum[2] tympanicum	paraquadrate	PQ
ossa petrosa	pro-otic (ossifications)	pro otische Verknöcherung *s.* regio pro-otica (petroso-occipitale)	pro-otic		pro-otic	PO
	epi-otics including opisthotics	regio epi-otica; regio opisthotica	epi-otic including opisthotic		opisthotic	OO
os occipitis partes laterales	exoccipitals	regio occipitalis lateralis	feebly developed occipital floor		exoccipital	EXO
os tympanicum	quadrate (ossification)	kleine, am Ende des Quadrat-knorpels auftretende Verknöcherung	suspensorium, ossified part		quadrate	Q
operculum	stapes	operculum mit columella	stapes		operculum	O
maxilla inferior	dentary	dentale	dentary		dentale	DENT
		angulare	articulare		angulare	ANG
	splenial	operculare			spleniale	SPL
lingulae cartilagineae	trabeculae	Trabekel; Schädelbalken	trabeculae		trabeculae	tr
cartilago ethmoidea	internasal fusion of trabeculae	unpaare Platte	internasal cartilage		internasal plate	in
		vorderste Ausläufer der Trabekel	trabecular cornua		rostral processes	r
	antorbital processes	Antorbital-fortsatz	ethmo-palatine element, or antorbital element		antorbital process	ao
saccus vestibuli	auditory capsules	Labyrinth-kapsel; pars cartilaginea	ear capsules		otic capsule	ot
parva lamina cartilaginea ossis occipitis		supra-occipitale Knorpel-platte	super-occipital band		supra-occipital arch	so
os occipitis — pars basilaris		basi-occipitale Knorpel-platte	an ossified bridge of cartilage		basi-occipital arch	bo

[1] The form given here is taken direct from the text of the author cited, and may be in one case the plural and in another the singular form, or may be used as an adjective. These differences are of course without significance.

[2] Gaupp, in suggesting the term "paraquadratum" leaves open a possible, or even probable, homology with the tympanicum of mammals, and in the frog has so named the corresponding bone.

The Appendicular Skeleton.

Shoulder Girdle.

The shoulder girdle consists of a pair of thin plates, almost entirely cartilaginous, wrapped about the sides of the body near the anterior end of the trunk, and entirely disconnected from other parts of the body skeleton and from one another. At about the middle of each plate is situated the glenoid fossa for the reception of the head of the humerus, and from this as a center there radiate three processes or lobes, one extending dorsally and two ventrally. The dorsal or scapular extension is narrow at its origin but broadens out towards its free end into a hatchet-shaped piece which extends as far dorsally as the transverse processes of the vertebrae. The narrow part of this extension becomes ossified to form a scapula, in shape something like the diaphysis of a shaft bone, with a constricted middle portion and two broadened ends; beyond this ossification the hatchet-shaped piece remains as a cartilaginous suprascapula. Of the two ventral extensions, the anterior, or procoracoid, is long and narrow and directed nearly anteriorly, while the posterior, or coracoid, forms an almost circular flat plate closely applied to the myotomic muscles on the ventral side of the thoracic region and extends so far beyond the median line that the coracoid of one side considerably overlaps the other, the left being usually the ventral or superficial one.

The cartilage, which is thin in most regions, is considerably thickened about the glenoid fossa both to strengthen the region and to allow sufficient depth for the reception of the head of the humerus. Externally, the thickened portion forms a definite ridge or lip nearly surrounding the fossa, being deficient only for a small space upon the anteromedial aspect.

Midway between the glenoid fossa and the re-entrant angle formed between procoracoid and coracoid is seen a small foramen coracoideum through which passes the supracoracoid nerve on its way to supply the muscles upon the ventral surface of the shoulder girdle. C. K. Hoffmann has pointed out that in the Anura this nerve lies in the interval between the procoracoid and coracoid, while here it bores through the cartilage, and that the result is brought about in the former case by a deepening of the incision between the two elements in question far enough to include the region of the foramen.

When the shoulder girdle is in its proper relationship to the body, the coracoid extends from the second to the fourth myocomma, and hence the largest of the sternebra, the one connected with the fourth myocomma, is situated exactly at the point at which the posterior margins of the two coracoids diverge from one another, a relation precisely similar to that of the sternal plate of the higher Urodela and of the arciferous Anura (*e. g.*,

Bombinator). This gives a suggestion of homology between the later amphibian sternum and the sternebrum of the fourth myocomma alone, the shape and extent of which frequently remind one of the well known rhomboid plate of such a form as Salamandra.

The procoracoid extends anteriorly as far as the first myocomma and its free anterior end is frequently covered by the transverse fold formed by the posterior border of the intermandibular muscle (M. intermaxillaris of authors).

Pelvic Girdle.

The pelvic girdle consists of a flat ventral plate, the pubo-ischium, and two lateral pieces, the ilia, attached to the sacral vertebra by means of a pair of ribs. The ventral plate has an elongated pentagonal outline similar to that shown by the skull but with its longitudinal axis still more prolonged. The anterior median angle is especially tapering and extends along the mid-ventral line of the abdomen but shows no trace of an epipubic cartilage (cartilago ypsiloides) as in so many Urodeles. The ilia are attached along the posterior lateral sides and at their bases are situated the acetabula for the reception of the heads of the femora. As in the case of the skull, the posterior margin is slightly incurved and its outer angles (corresponding in position to the mastoid processes of the opisthotics) are somewhat prolonged and tuberculate, forming the tuberosities of the ischia. At about the middle of the pubo-ischium are seen two small obturator foramina which may be used as indicative of the boundary between the pubic and ischiadic elements which are here otherwise unmarked. A pair of osseous areas situated in the posterior half, and which develop and increase in size during growth, plainly represent the osseous ischia. The growth of these is well marked by concentric lines. The middle portion of the ilium is also ossified, the bone being a little curved and with a rounded dorsal, and a broad and flat ventral end.

The ventral face of the pubo-ischium shows a slight muscular ridge along the middle line, and the dorsal or inner face is considerably excavated to form a pubo-ischiadic fossa for the accommodation of some of the viscera. The floor of the acetabulum is usually broken through by an acetabular foramen which leads into this last mentioned fossa.

The lateral view (pl. 65, fig. 13) shows the manner in which the ilium is attached to the sacral rib. Instead of meeting end to end and forming a definite joint, the cartilaginous ends of the two are prolonged and tapering and are applied to the sides of one another and held in place by firm connective tissue. The relations of this attachment to the vertebrae have been considered above under the vertebral column. In two cases which I have seen, a second ligamentous attachment appeared upon one side, extending

from the rib previous to the sacral rib to the dorsal end of the ilium; and in one of these which I have had the opportunity of examining more closely, the sacral rib on the right is normal and attached to what is probably the 19th vertebra, while the sacral rib upon the left side proceeds from the next posterior vertebra (20th). In addition to this, a strong but narrow ligament proceeds from the free end of the previous rib (19th) and inserts upon the dorsal end of the ilium anterior to the attachment of the sacral rib. As this fragment came from a student's preparation, the remainder of which had been lost, the exact determination of the vertebrae cannot be made, but judging from the other cases of oblique attachment which have been reported, the numbering is undoubtedly as given. This case resolves itself into one of "oblique attachment," such as have been reported by G. H. Parker, Waite, and Bumpus, the obliquity being dextro-sinistral (see above, under *Vertebral Column*).

The Free Limbs.

The serial homology between the fore and hind limbs in Necturus is very striking, and in so primitive an animal, perhaps the most primitive one possessing a cheiropterygium, points to a fundamental similarity of origin. It is thus of greater morphological interest than correspondences in such modified structures as the paddles of Ichthyosaurus where it is likely that the similarity is a secondary modification due to a similar method of use. This resemblance, which is apparent externally, is still more emphasized by the skeletal parts, and it seems incongruous to find such similar free limbs attached to such different girdles. Each limb terminates in four digits, the lost member being generally considered to be the first, and the phalangeal formula, 2–2–3–2, is the same in both manus and pes.[1]

With the exception of carpus and tarsus, which are wholly cartilaginous, the limb bones of the adult consist each of a bony shaft running through the middle, and two cartilaginous epiphyses, a slight exception being the terminal phalanges which are without epiphyses at the distal end. The shaft, or diaphysis, ossifies perichondrially, as always in the Amphibia, and forms a tubular sheath of bone, thick and constricted in the middle of its length and tapering at the ends to thin edges, the whole mass being something like the centrum of a biconcave vertebra considerably prolonged in the direction of its length. The epiphyses always remain purely cartilaginous, and never obtain calcareous deposits as in the frog.

[1] On this point Cope ('89, p. 25–28) seems to have made a singular mistake, giving the phalangeal formula for *N. maculatus* as 1–3–3–2 for the manus; and 1–2–2–2 for the pes. For the rare Carolina form, *N. punctatus*, he gives the formula 2–2–3–2 for both limbs, which corresponds to the normal condition in *N. maculatus* and is undoubtedly characteristic of the entire genus.

The limbs when in the normal resting or swimming position are directed backwards, and are held in such a way that in the hind limbs the soles face inwards, while in the fore limbs the dorsal surface of the manus is ventral, and the palm dorsal. This is apt to cause considerable difficulty in orienting the parts, but if the action of the limbs be watched in a living animal it will be seen that this position is due, not so much to a torsion, as to a swinging of the entire limb at the shoulder. The position assumed by the fore limb is the easier to understand, and in this it is evident that the limb when extended forward as in walking, rests with the palm down and the dorsal surface of the manus up, but that when the entire limb is swung from the shoulder so as to change its direction and point backwards, the positions of palm and dorsum are necessarily reversed. In the hind limb there is some tendency to counteract this by a torsion of the limb about its own axis and thus in a trailing hind foot the sole is turned somewhat inward.

Humerus.— The humerus, like the other long bones of the limbs, consists of an osseous shaft and two cartilaginous epiphyses. The usual cylindrical shape is retained only at the middle while the ends are both strongly flattened, and at right angles to one another, the proximal end being flattened laterally, and the distal end dorso-ventrally. The most prominent part of the proximal epiphysis is the head, which fits into the glenoid fossa of the shoulder girdle and forms the characteristic ball-and-socket joint. It is subspherical in shape, and is slightly affected by the general flattening of the entire region. Its ventral face is prolonged into a sharp ridge which is continued by the osseous diaphysis and forms one of the most distinctive features of the bone. This is the crista ventralis (crista deltoidea of Ecker) and serves for the insertion of most of the ventral shoulder muscles. This crest is highest near the junction of cartilage and bone and rapidly recedes, so that at the middle of the diaphysis no trace remains.

The distal end, which is broadened laterally and flattened dorso-ventrally, bears an extensive median furrow running around the end and up both surfaces, and dividing it into two masses which may be distinguished as the external (lateral) and the internal (median) condyles, although they include parts which in higher forms are distinct from the condyles themselves. The external condyle is somewhat the larger and is ball-shaped, fitting into the socket in the head of the radius. It also serves as a point of origin for the extensor muscles of the forearm and hand. Having these two functions, it plainly corresponds to both the external condyle and the capitulum of higher animals (epicondylus medialis and eminentia capitata of the frog; Gaupp).

The internal condyle is more nearly the exact homologue of the part of that name in higher forms as it gives origin to the flexor muscles of forearm and hand, but does not participate as directly in the formation of the elbow joint. The groove between the two condyles lies in the greater sigmoid notch of the ulna, and the olecranon of the ulna and

the capitulum of the radius fit respectively into its dorsal and ventral continuations during forced extension and flexion of the forearm. These slight grooves or depressions, of which the ventral is, perhaps, a little stronger than the dorsal, are thus the first suggestions of the olecranar and cubital fossae which develop in higher forms.

The humerus is distinguished from the femur by its sharp crista ventralis which projects farther than that of the femur and is differently shaped. This same feature, which marks the ventral side, and the large and spherical external condyle serve to orient the humerus.

Femur.— The general shape of the femur is like that of the humerus, but without much flattening at the proximal end. Here it shows two projections for muscular attachment: (1) a distinct process, mostly formed by bone, but tipped with a cartilage which in the adult is independent of the main epiphysis, and (2) a ridge or crest upon the side of the head, involving also a part of the shaft. It is somewhat difficult to compare these two distinct features with the single crista ventralis of the humerus, but in accordance with position it would seem that the bony process corresponds most closely with that part, and may thus bear the same name, while the ridge which lies more upon the external lateral aspect may be designated as the crista lateralis. As this crest is similar in appearance, though not in position, to the proximal cartilaginous part of the crista ventralis of the humerus, it is possible that these two parts found in the femur correspond to the single process of the humerus, and that in the former a difference in motion and consequently in muscular insertion has separated the two parts and diverted one of them from its original position. Such an explanation is, however, not in accord with the almost universally greater differentiation of the anterior limb, and one would expect to find in the femur the more primitive condition. Hoffmann distinguishes in the Urodeles a single projection referred to as crista femoris, a name applied by Gaupp to a similar part in the frog, but the femur of this latter animal is so unlike that of Necturus that homologies of parts are uncertain. It hence seems better to refer to the two processes found in Necturus by the two terms given above, crista ventralis and crista lateralis, terms which accurately express the position of the parts, and one of which suggests a justifiable homology with the humerus of the same animal.

The distal joint is imperfectly divisible into the external and internal condyles, although there is no distinct groove between them. The internal condyle is larger and longer and serves as the main point of origin for both flexor and extensor muscles of the lower leg and foot. The smaller external condyle articulates with the proximal end of the fibula.

The osseous crista ventralis, separated from the head by a notch, is sufficient to distinguish femur from humerus and to mark the ventral side of the bone. This and the more projecting internal condyle of the distal epiphysis will complete the determination.

Antibrachium and manus; crus and pes.— These parts in the two limbs are almost indistinguishable from one another, as may be seen by a comparison of figures 14 and 15 (plate 66), which were drawn from the right anterior and posterior limbs of the same individual by the aid of a camera lucida. Corresponding to a difference in use of elbow and knee, the proximal ends of ulna and radius are different from those of tibia and fibula, but otherwise the parts correspond as closely as do consecutive parapodia of a polychaetous Annelid.

The ulna shows a greater sigmoid notch and the radius a capitulum, both for the reception of parts of the distal epiphysis of the humerus. Furthermore, these bones are a little longer than are the tibia and fibula. Carpus and tarsus are exact duplicates in the two limbs and consist of two proximal bones, a centrale, and three bones of the distal row. In the proximal row the intermedium is fused with the outer element (ulnare or fibulare), leaving between them a foramen for the transmission of an artery.[1] In the distal row, digits II and III have each a distinct element, while those corresponding to IV and V are fused. Four digits, II–V, are represented in each case, each with a well developed metacarpal or metatarsal and nine phalanges, three in the fourth digit and two in each of the others. Three phalanges in the third digit, also, is a not uncommon anomaly.

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[1] The artery in the hand which runs through the foramen carpale is the art. cubitalis which thus reaches the dorsal surface and is distributed to the digits. In the foot a similar function is performed by the continuation of the art. femoralis.

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Explanation of Plates.

(The outlines of all the figures were drawn with a camera, three times the natural size in the majority of the cases. Since, however, the originals varied considerably in size, the resulting figures cannot be considered as proportionate to one another. The figures of the chondrocranium, for example (pl. 63, figs. 4, 5), were drawn from a very small specimen and enlarged four times, but the resulting figures are almost exactly comparable with those of the entire skull (pl. 63, figs. 2, 3) drawn from a medium sized specimen at a magnification of but three diameters. A large skull at two diameters would give about the size of figures 2 and 3.)

ABBREVIATIONS USED.

(The abbreviations given in the following list include those used in the figures, as well as those employed in the text at various places.)

1. Bones.

A — atlas.
ANG — angulare.
BB — basibranchiale 2
CS — costa sacralis.
DENT — dentale.
EXO — exoccipitale.
F — frontale.
FB — fibula.
FM — femur (diaphysis).
H — "1st haemal arch vertebra" (see text).
HM — humerus (diaphysis).
IL — ilium.
IS — ischium.
MC — metacarpalia.
MT — metatarsalia.
OO — opisthoticum.
OP — operculum.
P — parietale.
PB — parabasale.
PH — phalanges.
PMX — premaxillare.
PO — pro-oticum.
PPT — palato-pterygoideum.
PQ — paraquadratum.
Q — quadratum.
R — radius.
S — sacrum.
SC — scapula.
SPL — spleniale.
T — tibia.
UL — ulna.
V — vomer.

2. Other Designations.

Abbreviation. *Name.*	*Location.*
a. b–o. — arcus basi-occipitalis.	
art. — articulare (Meckel's cartilage).	
a. s–o. — arcus supra-occipitalis.	
b. b. 1. — basibranchiale 1.	
br. — bronchus.	
c. — carpalia.	
caps. nas. — capsula nasalis.	
caps. opt. — capsula optica.	
caps. ot. — capsula otica.	
cart. lat. — cartilago lateralis.	
cart. Mk. — cartilago Meckelii.	
c. b. 1–2. — ceratobranchiale 1 et 2.	
cent. — centrale.	
c. h. — ceratohyale.	
cond. ext. — condylus externus.	H and FM.
cond. int. — condylus internus.	H and FM.
cond. oc. — condylus occipitalis.	EXO.
cor. — coracoideum.	
cr. lat. — crista lateralis	FM.
cr. mus. — crista muscularis.	Pelvic girdle.
cr. temp. — crista temporalis.	F.
cr. ventr. — crista ventralis.	H and FM.
e. b. 1–4. — epibranchialia 1–4.	
epiph. c. s. — epiphysis costae sacralis.	
epiph. il. — epiphysis ilii.	
f. acet. — foramen acetabulare.	
f. carp. — foramen carpale.	
f. cor. — foramen coracoideum.	
f. mand. — foramen mandibulare.	
f. obtur. — foramen obturatorium.	
f. sty.-m. — foramen stylo-mastoideum.	
f. tars. — foramen tarsale.	
fib. — fibulare.	
fn. oval. — fenestra ovalis.	

Abbreviation. Name.	*Location.*
foss. acet.— fossa acetabularis.	
foss. glen.— fossa glenoidalis.	
foss. olec.— fossa olecrani.	
foss. pub.-isch.— fossa pubo-ischiadica.	
h.-h.— hypohyale.	
int.— intermedium.	
isch.—ischium (cartilaginous).	
isth.— isthmus.	
lig. hyo-sus,— ligamentum hyo-suspensoriale.	
lig. md-hy. ext.— ligamentum mandibulo-hyoideum externum.	
lig. md hy. int.— ligamentum mandibulo-hyoideum internum.	
marg. ventr. — margo ventralis.	Of anterior naris.
nar. ant.— naris anterior.	
p. a-l.— proc. antero-lateralis.	P.
p. a-m.— proc. antero-medianus.	P.
p. a-o.— proc. antorbitalis.	
p. ang.— proc. angularis.	ANG.
p. ant.— proc. anterior.	SPL.
p. artic.— proc. articularis.	Q.
p. asc.— proc. ascendens.	q.
p. colum.— proc. columellaris.	OP.
p. cor.— proc. coronoideus.	ANG.
p. mast.— proc. mastoideus.	oo.
p. oo.— proc. opisthoticus.	P.

Abbreviation. Name.	*Location.*
p. operc.— proc. opercularis.	PQ.
p. orb-sph.— proc. orbito-sphenoidalis.	P.
p. ot.— proc. oticus.	Q+q.
p. par.— proc. parietalis.	F.
p. pmx.— proc. premaxillaris.	F.
p. p o. — proc. pro-oticus.	P.
p. pt. — proc. pterygoideus.	q.
p. q.— proc. quadratus.	P.
p. q. d.— proc. quadratus dorsalis.	PO.
p. q. v.— proc. quadratus ventralis.	PO.
p. r.— proc. rostralis.	
p. uncin.— proc. uncinatus.	F.
pc.— procoracoideum.	
ped.— pediculus.	q.
pl. int.-nas.— planum internasale.	
pub.— pubis.	
pul.— pulmo.	
q.— quadratum (cartilage).	
rad.— radiale.	
ss.— suprascapula.	
sym.— symphysis mandibulae.	
t.— tarsalia.	
tib.— tibiale.	
trab.— trabecula.	
trach.— trachea.	
tub. isch.— tuberositas ischii.	
uln.— ulnare.	

PLATE 62.

Figs. 1a, 1b. Vertebral column. $\times 1\frac{1}{2}$. The view is a dorsal one as far as the sacrum, beyond which it becomes twisted so as to expose the right side of the flattened caudal region. The break between vertebrae 34 and 35 indicates that the detached piece was drawn from a second specimen, but one in which the identity of the vertebrae was known.

A — atlas ; S — sacrum ; H — the first vertebra showing a complete haemal arch.

PLATE 63.

Fig. 2. Dorsal view of skull with nasal capsules removed.

Fig. 3. Ventral view of same.

Fig. 4. Dorsal view of chondrocranium with its cartilage bones.

Fig. 5. Ventral view of same.

PLATE 64.

Fig. 6. Nasal capsule in place ; dorsal view.

Fig. 7. Internal aspect of left mandible.

Fig. 8. External view of same.

Fig. 9. Details of the otic capsule and suspensorium ; ventral view of right side. Some of the parts are slightly separated.

Fig. 10. Dorsal view of suspensorium (quadratum).

Fig. 11. Ventral view of same.

PLATE 65.

Fig. 12. Ventral view of head and neck regions, showing visceral arches.

Fig. 13. Lateral view of pelvic girdle, with attachment to vertebral column.

Fig. 14. External lateral view of right humerus.

Fig. 15. External lateral view of right femur.

PLATE 66.

Fig. 16. Ventral view of right shoulder girdle.

Fig. 17. Lateral view of right shoulder girdle.

Fig. 18. Forearm and manus; dorsal view of right.

Fig. 19. Lower leg and pes; dorsal view of right.

PLATE 67.

Fig. 20. Ventral view of pelvic girdle.

Fig. 21. Dorsal view of pelvic girdle.

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H. H. Wilder, del.

Wilder, Skeletal System of Necturus.

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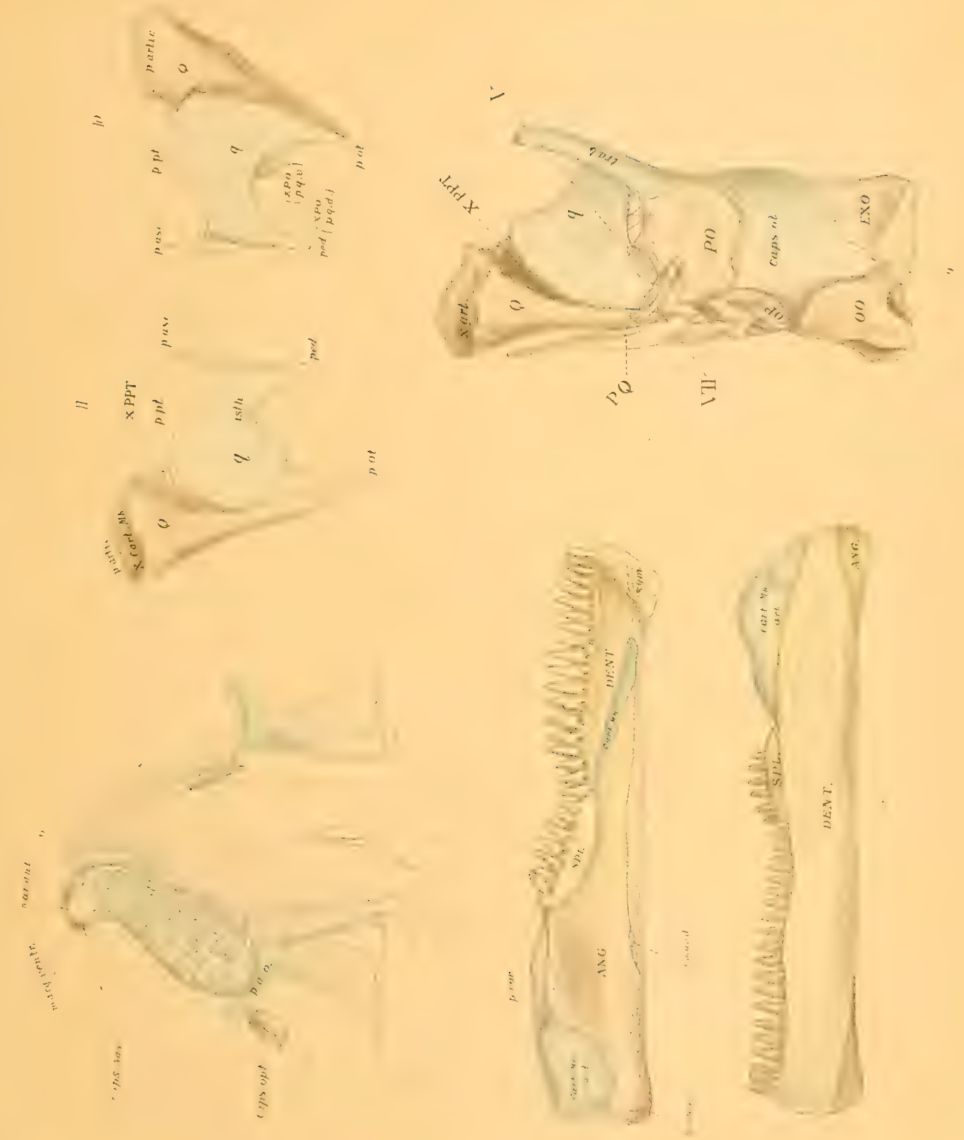


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SKELETAL SYSTEM OF NECTURUS